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Memoirs of the Museum of Comparative Zoölogy  
AT HARVARD COLLEGE.  
VOL. XL. No. 5.

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ZAGLOSSUS,  
CAMBRIDGE, MASS.

BY  
GLOVER M. ALLEN

WITH TWO PLATES.

CAMBRIDGE, U.S.A.:  
Printed for the Museum.  
OCTOBER, 1912.



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# ZAGLOSSUS.

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## INTRODUCTION.

SINCE its discovery in 1876, specimens of the Long-beaked spiny anteater of New Guinea have been rare in collections. Hitherto the osteology of but a single specimen has been completely known, and of the anatomy of the soft parts practically nothing has been published. No less than five forms have been described, but the validity of most of these seems questionable, and even the genus itself is by some considered unworthy of recognition.

The Museum has lately acquired seven specimens, four skins with skulls and three aleoholies, which together with a mounted skin purchased many years ago, and a mounted skeleton kindly loaned by the United States national museum, appear to constitute all the available material in America. On the basis of this material I have prepared the following review of the history and characters of this interesting monotreme.

## HISTORY AND NOMENCLATURE.

Peters and Doria (1876) based their original description of the Proechidna on a cranium from Mt. Arfak, northern New Guinea. It lacked a large part of the posterior end as well as the lower jaw, but from its strikingly long and curved rostrum as compared with that of the Australian Eehidna, they considered it a new species and named it *Tachyglossus bruijnii*. In the Annual record of science and industry for 1876, p. clxxi, published about May 5, 1877, Gill called attention to this new and remarkable animal and proposed for it the generic name *Zaglossus* (see Palmer, 1895). Gervais, in November, 1877, unaware of Gill's paper, likewise considered it generically distinct from *Tachyglossus* and named it *Acanthoglossus*, which he shortly discovered was preoccupied by *Acanthoglossa* for a genus of insects. He accordingly renamed it *Proechidna*, under which title it has become generally known. Indeed the name is so well established that it seems best to retain it in a vernacular sense, as well as the

name Eehidna for *Tachyglossus*. Dubois (1881) considered *Acanthoglossus* sufficiently distinct from *Acanthoglossa* but in case this view were not accepted, he proposed the name *Bruynia* instead, with *tridactyla* as the specific name. In the Zoölogical record for 1882, Thomas amends this to *Bruijnia*, and adopts the combination *Bruijnia bruijnii*, though in the year following he reverts to *Proechidna bruijnii* which is the name finally used in his Catalogue of the Marsupialia and Monotremata in the British museum (1888). More recently, in conformity with his adherence to the 'one-letter rule,' Mr. Thomas (1907) has considered *Acanthoglossus bruijnii* the correct name, but Palmer (1895) has called attention to the name *Zaglossus* of Gill, which though long overlooked, must evidently take precedence if the *Proechidna* be considered generically distinct from the *Eehidna*. On this latter point there has been much difference of opinion, but as later detailed, there seems sufficient ground, as modern generic conceptions go, to keep the two apart.

There is still some doubt as to the number of local races or species of *Proechidna* in New Guinea. Under the name *Proechidna villosissima* Dubois (1884) figured and described an animal from northern New Guinea which he believed to represent a second species. It was evidently an immature specimen from its small size (total length, 390 mm., rostrum 61), had a nearly straight beak, and a very woolly thick pelage of a uniform dull brown. The spines are described as white and needle-like, not exceeding 19 mm. in length, and almost completely hidden in the fur, except that their extreme tips project from the woolly covering at the sides of the neck and in the caudal region. There were sixteen pairs of ribs, one less than recorded by Gervais, but a number probably normal for the genus as I shall later show. Owing to the evident youth of this specimen it has been regarded by most authors (and I think rightly) as merely an immature *bruijnii*. Gill (1885) in calling attention to his earlier use of the name *Zaglossus*, includes *Zaglossus villosissimus* as a second species of the genus, but evidently he had not seen a specimen. Rothschild (1892) considered it a variety of *bruijnii* and later (1905) in reviewing the genus recognized it definitely as a subspecies of that animal. This review was based on a study of nine specimens, more than had previously been brought together by any investigator. Rothschild believed that three forms were recognizable:—(1) *Zaglossus bruijnii* with brownish black or black hair, and white spines; (2) *Zaglossus bruijnii villosissima* with pale brown hair, thick, long, and woolly, hiding the spines except on flanks and shoulders; and (3) *Zaglossus bruijnii nigroaculeata*, described by the same author in 1892 as *Proechidna nigroaculeata*, which has uniformly dark, long, thin, and

bristly hair, and black somewhat flattened spines. No cranial characters are given as the specimens were unaccompanied by separate skulls.

In 1907, Thomas obtained a specimen of this genus from Mt. Victoria, British New Guinea, at an altitude of 8,000 feet, the first known from this portion of Papua. It was an old female, but the cranial measurements, though large, do not exceed those of Gervais's larger specimen. This specimen is made the type of *Acanthoglossus bruijnii bartoni* and is briefly characterized as having fur long and thick, entirely hiding the spines over the whole of the dorsal area except on the nape, sides of the neck, flanks, back of rump, and caudal region. The general color is black throughout except the hands and feet which are brown grizzled with whitish. The spines are white, thin, not exceeding 30 mm., and are absent from the belly. It is not clear how this is to be distinguished from the race *vilosissima*, except that it is black instead of brown. This difference, however, is probably individual. In the same year Thomas (1907a) described *Acanthoglossus goodfellowi* as a new species from the island of Salawatti. This specimen was obtained from the natives who may quite readily have brought it to this island from the adjacent shores of New Guinea. Salawatti is a rather low island separated from Papua by a narrow stretch of mud-flats, and its fauna so far as known is not different from that of the Papuan mainland. The species is said to be easily recognizable by the predominance of the spines and the almost entire suppression of the woolly coat. The longest spines are some 30 mm. in length, and are white shading basally to gray. The fur is short and scanty, of a uniform black throughout. The skull presents no marked peculiarities. All these characters are shown in one of our Papuan examples, so that there seem to be no grounds for recognizing a Salawatti race, even in case it should be true that the animal naturally occurs there and was not carried thither by the natives. Thus though there are currently recognized five varieties of the Proechidna the validity of more than the one species is open to serious question.

#### EXTERNAL CHARACTERS.

In the eight specimens in the collection of the Museum of Comparative Zoölogy all the characters claimed for these described races are to be found in various combinations, yet there seems no good reason for recognizing more than one form among them. The color of *Z. bruijnii bruijnii*, as stated by Rothschild, is brownish black or black. The head may be paler than the body, or in albinistic individuals may be more or less white. No. 6,722 M. C. Z. is

partially albinistic. It has the head from the base of the rostrum back nearly half the distance to the ear opening, white, a white spot on the right side in front of the shoulder, another on the left side behind the shoulder, and an irregular series of marks on the rump. It is evident that such marks are of no taxonomic value in the present case. No. 7,398 M. C. Z. is a topotype from Mt. Arfak, and is preserved in alcohol. The face, forehead, limbs, and belly are a dark Vandyke brown, darkening to seal-brown over the dorsal region. The fur is thick and woolly, but the spines project conspicuously above it. These spines are uniformly blackish with white tips, are short on the occiput but large over the back, shoulders, and caudal region where the longest reach nearly 37 mm. They encroach slightly on the sides of the venter, but are few and scattered on the belly. Thomas (1907a) says that in *bruijnii* the belly is without spines throughout but this is hardly the case in any of the specimens I have examined. In its possessing black spines this specimen resembles "*nigro-aculeata*," but it is not so thinly haired as Rothschild describes. The flattened character of the spines in this supposed race is unquestionably the result of wear. For in an old specimen, M. C. Z. 12,414, many of the dorsal spines are worn quite to the small hollow center and have become beveled off nearly flat on their dorsal surface. This old specimen consists of a skin and skeleton from Fak Fak, New Guinea. The hair and spines are greatly worn and so scattered that the skin is everywhere visible. The general color of the hair on the fore part of the head is a pale buffy, but on the dorsal part of the body the scattered bristles are blackish or blackish brown. Those on the ventral surfaces are a more decided brownish, near Prout's brown. On the fore limbs are a number of grizzled whitish hairs with the brown. Of the spines, almost all are white throughout but a few, on the shoulders, back, and hips are blackish, with pale bases. The ventral spines are short and are distributed from the axilla nearly to the groin. They are arranged in rather definite curved rows, the most anterior passing posteriorly and dorsally, the later rows curving laterally from the axilla, then in towards the groin. These ventral spines reach to within 25 mm. of the midline. This large specimen is apparently identical in general characters with that described by Thomas (1907a) as *Acanthoglossus goodfellowi* from the island of Salawatti. There can be little doubt that both are simply old animals with the hair either much worn or partly shed. Of much interest in our specimen is the fact that among the large worn spines are scattered other smaller ones, sharp-pointed and unworn, that appear to be new spines coming in.

In 12,415, M. C. Z., an adult also from Fak Fak, the spines are large, stout,

prevailingly white, and almost unworn, the longest reaching 44 to 47 mm. on the rump. The coarse brown hair which covers the upper part of the body rather thickly, has the appearance of being much worn and broken allowing the spines to project nearly their entire length, with the result that the animal appears much more spiny than those in which the hair is unworn and covers the bases of the spines.

Two specimens from Sorong, New Guinea (M. C. Z. 7,009, 7,010), presented by Dr. Thomas Barbour, agree in having the hair of the body nearly coal-black, with the bases more or less brownish. The larger spines vary from dark horn color to blackish, the smaller ones are entirely black save for a few very small spines on the occiput which are white. The venter is nearly free from spines.

It seems evident from a study of the material in the collection of the Museum, that the characters claimed for the races *nigroaculeata* and *goodfellowi* are individual or the result of age and wear. Moreover no geographical limits are established for these variations. So, unless other and more distinctive characters can be found, it seems unnecessary to consider these as valid races.

With regard to the race *vilosissima* there seems also room for much doubt. The original specimen described by Dubois (1884) appears from its measurements to have been immature, which would account for its short and nearly straight rostrum. The chief character claimed for it is the long and woolly hair, completely hiding the spines except on the sides of the neck and in the caudal region. It appears, however, that the longest spines did not exceed 19 mm., which is about half the length of those of adult *bruijnii*.

The collection of the Museum contains a Proechidna from Mt. Arfak, M. C. Z. 7,397, the type locality of *bruijnii*, that agrees with the description of *vilosissima* in having the pelage notably thick and woolly. The spines, however, are slightly longer than described for *vilosissima* (21 to 24 mm.) and although most prominent on the shoulders and rump, project slightly above the hairy coat. They are black, or black with light tips, instead of white as described. The skull shows the specimen to be very immature, and it is undoubtedly the youngest of the eight skulls examined. In almost every respect it is identical with immature skulls of *bruijnii*, but differs from all those studied in that the anterolateral terminations of the large interparietal are each in contact with one of the nasals. In the four other specimens of *bruijnii* in which these bones are still traceable, the interparietal does not abut against the nasals, although in two cases, the distance separating the two bones is not over 5 mm. Probably therefore this character is merely individual. Rothschild

(1905) states that in his series of nine Proechidnas are specimens even more thickly haired than Dubois claimed for the type of *vilosissima*, but adds that he and Dr. Hartert differed as to which should be considered young animals, for there was no way of comparing the skulls. The dense character of the pelage may be retained in the adult, as is the case apparently of the specimen from British New Guinea, made the type of the race *bartoni* by Thomas. The thickness of the hairy coat can not of itself be considered a specific character since even the small series of specimens at hand shows much variation in this respect. Possibly the extreme condition shown by the *vilosissima* specimens is in part a concomitant of youth, as has been suggested by earlier writers. The lack of definitive cranial characters, together with the absence of trenchant differences in external features or geographical range, seems sufficient ground for relegating *vilosissima* to synonymy under *bruijnii*.

To recognize four or five races of Proechidna all of which may occur together in the western peninsula of Papua seems a rather anomalous proceeding, particularly since these are not separated by any structural peculiarities. The case is somewhat paralleled by that of the Australian Echidna in which the range of variation is so great as to have led at various times to the recognition of several races, although now but one form is accorded to that continent. While I have not seen the type of either *bartoni* or *goodfellowi*, a careful study of the descriptions of these two races does not reveal any diagnostic characters, and it seems best to consider these names for the present, at least, as synonyms.

As long ago as 1868, Krefft reported the discovery of Echidna-like remains in the Wellington bone and breccia caves of New South Wales, Australia, and he figured a portion of a humerus. Later, Owen made further reports on additional fragments discovered in these caves. He figured a nearly complete humerus that appears to belong to Zaglossus rather than to Tachyglossus as I shall later show. This important discovery points to the former coexistence of the two genera in Australia, and is of special interest in its zoögeographic bearing, since at the present day both are found in New Guinea; but the Echidna alone survives in Australia. It follows therefore that the Proechidna was already well differentiated from the Echidna long before Papua was sundered from Australia, so that it is not a recent Papuan derivative from an Echidna stock, developed here through isolation. But rather the two genera have long existed side by side.

The distinctive characters of the Australian fossil Proechidna are insuffi-

ciently known, so that although doubtless enough to entitle it to separate rank I am unable here to give them in detail.

I would recognize but one living form of Proechidna and one fossil, with the following synonymy.

**Zaglossus bruijnii bruijnii (PETERS and DORIA).**

*Tachyglossus bruijnii* PETERS and DORIA, Ann. Mus. civ. storia nat. Genova, 1876, **9**, p. 183.

*Zaglossus bruijnii* GILL, Ann. rec. sci. and industry, 1877, p. elxxi.

*Acanthoglossus bruijnii* GERVAIS, Compt. rend. Acad. sci. Paris, 1877, p. 837.

*Proechidna bruijnii* GERVAIS, Ostéogr. des monotrèmes, 1877 '78, fasc. 1, p. 43.

*Bruynia tridactyla* DUBOIS, Bull. Soc. zool. de France, 1881, **6**, p. 266.

*Bruynia bruijnii* THOMAS, Zool. record. 1882, **19**, Mammalia, p. 40.

*Echidna (Acanthoglossus) bruijnii* MURIE, Journ. Linn. soc. London, 1879, **14**, p. 413.

*Echidna bruijnii* FLOWER and GARSON, Cat. Mus. roy. coll. surgeons, pt. 2, 1884, p. 753.

*Proechidna villosissima* DUBOIS, Bull. Mus. roy. hist. nat. Belg., 1884, **3**, p. 110.

*Proechidna nigroaculeata* ROTHSCHILD, Proc. Zool. soc. London, 1892, p. 545.

*Zaglossus bruijnii villosissima* ROTHSCHILD, Novitates zoologicae, 1905, **12**, p. 305.

*Zaglossus bruijnii nigroaculeata* ROTHSCHILD, Novitates zoologicae, 1905, **12**, p. 305.

*Proechidna novaguineae* and *Proechidna leucocephalus* ROTHSCHILD, Proc. Zool. soc. London, 1892, p. 546 (nomina nuda, quoted from a dealer's catalogue).

*Acanthoglossus bruijnii bartoni* THOMAS, Ann. mag. nat. hist., 1907, ser. 7, **20**, p. 293.

*Acanthoglossus goodfellowi* THOMAS, Ann. mag. nat. hist., 1907, ser. 7, **20**, p. 498.

Habitat: Papua.

† **Zaglossus oweni (KREFFT).**

*Echidna owenii* KREFFT, Ann. mag. nat. hist., 1868, ser. 4, **1**, p. 114.

*Echidna ramsayi* OWEN, Phil. trans. Roy. soc. London, 1884, **175**, p. 273.

Extinct: Australia, New South Wales; remains in Wellington bone and breccia caves.

Attention may be called at this point to the studies of Toldt (1905, 1906) on the hair and spines of the Proechidna. He points out what may fairly be considered a generic difference in the character of the spines of the Proechidna as compared with the Echidna. For while in the latter they are thin-walled, with a relatively large lumen and long tapering point, in the Proechidna they are blunter and much more solid, with a very small central lumen. Toldt shows that a light-colored spine may have a concealed layer of dark pigment near its core; other spines are without pigment, and others again appear dark-pigmented. This, however, is a matter of individual variation for both light and dark spines may occur in the same animal or one or the other sort may predominate. The color of the spines, on which Rothschild seems mainly to have based his race *nigroaculeata*, can therefore have no systematic significance in this case. Toldt, however, prefers to consider his dark-spined individual *nigroaculeata*. The transition from hairs to various forms of spines is well brought out by this

author, who illustrates such a transitional series by hairs and spines selected from different parts of the same animal.

MEASUREMENTS.—The largest recorded Proechidna is that made by Rothschild (1892) the type of his *nigroaculeata*. This specimen measured in the flesh 31 inches (about 640 mm.) in total length. Dubois (1881) records an adult that measured 620 mm. from the tip of the snout to the tip of the tail. Two adult skins, M. C. Z., Nos. 12,414 and 12,415, measure 717 and 539 respectively, but there is no way of proving whether the specimens are overstuffed. Rothschild's measurement is probably nearly maximum for adults. Weber (1888) gives measurements taken from five skins but all are less than 640 mm.

The naked part of the rostrum in M. C. Z. 12,414, measures 101 mm. The claws of the left fore and hind feet measure:—

	Left fore foot.	Left hind foot.
Digit 2	22.6	47
Digit 3	27	38.7
Digit 4	25	28

The spur in this specimen is 7 mm. long.

A series of cranial measurements is given in the part of this paper dealing with the osteology.

#### MUSCULATURE.

MUSCLES OF THE SKIN.—As in the case of the Echidna, the *panniculus carnosus* is very remarkably developed, so as to form a loose muscular sac in which are imbedded the bases of the spines. By its contraction this muscle erects the spines, which thus form a bristling armament. Fewkes (1877) has described and named as separate muscles, several of the subdivisions of this enveloping sac in the Echidna, and the same divisions appear to be present in the Proechidna. Anteriorly the *panniculus* extends as far as the parietal region, whence its fibers extend diagonally forward just back of the eyes and pass transversely under the chin. Medially on the forehead there is a narrow space devoid of muscle fibers where the union of the two lateral portions of the muscle is by fascia only. There is an attachment also along the posterior part of the squamosal bone on each side. From the head, the fibers are continued on both dorsal and ventral sides of the body to the tail and laterally on to the legs. Dorsally the muscle is thickest midway between the median line and the ventral border of the body and forms a continuous sheet across the back where the

fibers of opposite sides, passing diagonally posteriorly and dorsally from the venter, meet along the median line. Here there is a narrow area devoid of spines that runs the length of the vertebral column. On the fore limbs the fibers extend to the carpus externally, but not quite so far on the radial side. They insert for a space of about 20 mm. on the distal ulnar margin and pass also into the fascia covering the hand. Posteriorly the fibers encircle the lower leg, below the knee and similarly become confluent with the fascia investing the extremity of the leg.

The following secondary attachments were found:—(1) a small muscular bundle, rather triangular in section, and divisible into two main strands, arises by a flat tendon from the posterior tuberosity of the head of the humerus, slightly internal to the insertion of the *pectoralis*, and passes dorsad and caudad some 65 mm. to the dorsolateral portion of the *panniculus*, with the fibers of which it becomes united. This is the *dermo-brachialis posterior* of Fewkes.

(2) A smaller and more nearly cylindric muscle takes origin by a separate tendon just external to the last, from the posterior tuberosity of the humerus; it is of about the same length, but curves distinctly cephalad. Its fibers run forward into those of the *pannieulus* at about the position of the large spines on the fore shoulder. Fewkes names this muscle the *dermo-brachialis anterior*.

(3) A thin sheet of muscle which appears to be the *dermo-cervicis triangularis* spreads over the back of the neck and inserts with the *panniculus* into the distal part of the ulna. The two muscles of opposite sides are continuous dorsally through a thin aponeurosis.

(4) What Fewkes has called a *dermo-dorsi cervicalis* in the Echidna exists also in *Zaglossus* (Plate 1, fig. 1, *m*). It arises just back of the shoulder by muscular strands from the eighth and ninth ribs, and is connected by aponeurosis with the posterior ends of the *trapezius* and the *latissimus dorsi*. These strands unite to form a flat muscle about 70 mm. long and 17 mm. wide at the point of insertion into the dorsal part of the *panniculus*. It passes anteriorly before uniting with the latter, and then expands to a width of some 34 mm. The muscles of opposite sides apparently do not unite to form an ellipse on the back such as Fewkes describes for the Echidna, but at their anterior approximation the two muscles are separated by about 10 mm. They are more or less intimately connected, however, with a thin sheet of non-muscular tissue that covers the dorsum. This sheet is attached along either side at about 30 mm. from the midline, from the eleventh rib and medially from the eleventh dorsal spine posteriorly. Toward the sides of the body it becomes thickened with fat and

finally forms a great layer of adipose tissue that extends from the axilla to the groin, next the body muscles.

(5) A very remarkable muscle, named by Fewkes the *dermo-flexor antebrachii*, arises by a series of digitations from the eighth to the thirteenth ribs (Plate 1, fig. 1, *ld*). The first of these is in contact with one of the slips of the *dermo-dorsi cervicalis*, at its ventral border. The entire muscle is somewhat fan-shaped and its fibers converge and pass to a tendinous insertion into the fascia investing the fore arm, about halfway on its ventral surface. Mivart (1866) considers this muscle a posterior portion of the *latissimus dorsi*, but as stated by Fewkes, its insertion is different, though its origin is similar. Mivart's supposition, however, has much to recommend it. From a lateral view it is seen that the origins of *latissimus dorsi*, *dermo-dorsi cervicalis*, and *dermo-flexor antebrachii* form a practically continuous series of digitations from the ribs, as is usual for the *latissimus*. What may once have been thus a single muscle, originating by digitations from the first to thirteenth ribs and inserting on the ulna, may quite conceivably have become broken into three sections, as here, the two posterior of which have become superficial in their attachments. The function of the middle portion (*dermo-dorsi cervicalis*) has thus become changed to that of a retractor of the bases of the dorsal spines, while the function of the posterior part (*dermo-flexor antebrachii*) is still practically that of the true *latissimus*, serving to approximate the fore arm while at the same time drawing it posteriorly. Owing to the great anteroposterior extent of the arm, the efficiency of the true *latissimus* is greatly lessened so that the transference of the insertion of this posterior portion from the ulna to near the carpal region results in a great gain of power for a burrowing animal.

(6) What are evidently the *dermo-extensores brachiales intimus, inferior, et superior* of Fewkes, are also present in Zaglossus as a narrow band of superimposed sheets about 10 mm. wide and 100 mm. long, from near the midline of the *panniculus* at the back of the neck, passing to the fasciated sheath that encircles the wrist and inserts on the ulna.

(7) A muscle named by Fewkes the *dermo-flexor cruris* (Plate 1, fig. 1, *dfc*) arises by a thin tendinous sheet from the spines of the coccygeal vertebrae, and is joined by a few fibers of the overlying part of the general *panniculus*. The broad sheet of muscle thus formed passes laterally and invests the lower hind limb where on the external aspect it becomes a thin sheath of aponeurosis and internally is muscular. From the distal part of this sheath a conspicuous muscle band is separated and passes to a tendinous insertion 7 mm. long on the

peroneal aspect of the tibia. A similar condition is described in the case of the Echidna by Fewkes.

**MUSCLES OF HEAD AND NECK.**—The muscles of the head appear to resemble those of the Echidna in all essential respects. The long snout is covered by thin hardened cuticle quite without any evident musculature. The muscles operating the lower jaw are also very poorly developed in correlation with the slight mobility of that member. There are therefore almost no facial muscles.

A thin flat muscle about 20 mm. wide arises by thin connective tissue from the parietal region under the anterior edge of the *panniculus* and passes to the posterior edge of the opening of the external ear. Its homology is not altogether certain.

The *digastric* muscle is a short narrow strand from the skull just anterior to the ear, to the posterior corner of the angle of the jaw.

The *masseter* is also inconspicuous, arising from the posterior half of the ventral margin of the zygomatic arch. It inserts in a shallow depression on the external side of the mandible from the angle of the jaw to a small prominence about 1 cm. in advance that may be considered a coronoid process. In the Echidna this muscle is described as considerably larger, with an origin about an inch in length, from a point "about half an inch in advance of the anterior edge of the orbital foramen."

The *temporalis* fills the posterior half of the orbit, where its origin is only about 1 cm. in length. It narrows to its insertion on the coronoid process.

Directly under and posterior to this is the *pterygoideus internus*, which arises from the skull by muscular fibers from the insertion of the *temporalis* to the glenoid cavity of the jaw. It inserts on the inner side of the jaw from the condyle to the coronoid process, and is about as large as the *temporalis*.

The *pterygoideus externus* is smaller and arises posterior to the *pterygoideus internus* and inserts on the inner side of the condyle of the jaw. The condition is apparently the same as in the Echidna, as minutely described by Lubosch (1906, p. 558). The homology of these muscles with the pterygoidei of other mammals is uncertain.

The *trapezius* muscles, as in the Echidna, consist of an anterior and a posterior. The former arises by a thin tendinous sheet from the entire midline of the neck and mainly from the side of the occiput, dorsal to the ear. It inserts along the dorsal half of the clavicle and the anterior edge of the scapula, where its fibers join those from the second or posterior portion at the anterodorsal

angle. Possibly this anterior part may represent an *acromio-clavotrapezius*. The insertion seems to be slightly less extensive in the Echidna.

The posterior portion of the *trapezius*, perhaps the homologue of the *spino-trapezius* is a flat sheet, nearly an equilateral triangle in outline, arising by a very thin tendinous sheet from the dorsal spines of the tenth thoracic to the second lumbar vertebrae. It thickens greatly as it narrows to its insertion, some 20 mm. in length, on the anterior edge of the scapula (the region corresponding to the spine).

As in the Echidna, the *rhomboideus* is a single muscle, arising under the *trapezius* from the parietal margin of the skull, above and slightly in advance of the ear, nearly to the midline of the cranium, and posteriorly underneath almost the entire length of the *trapezius*. It thickens as it passes laterally to its insertion along the entire vertebral border of the scapula.

The *levator scapulae ventralis* arises by two heads:—(1) a slightly tendinous attachment from the basioccipital and (2) a strong muscle mass from the ventro-lateral portion of the atlas and axis. The insertion is at the anterior edge of the scapula at the point of union with the clavicle and thence dorsally for about 20 mm. Mivart (1866) in the Echidna did not note the extension of the origin to the axis, but otherwise the muscle appears to be similar.

The *occipitosepularis* is a narrow ribbon-like muscle from the mastoid region just posterior to the ear. It is inserted along the vertebral edge of the scapula, beginning about 10 mm. from the gleno-vertebral angle and extending anteriorly about twice that distance. Apparently Mivart (1866) and Westling (1890) did not find this muscle in the Echidna.

The *cleidomastoideus* is wanting as in the Echidna.

The *latissimus dorsi* has already been mentioned in connection with the cutaneous muscles. It may be considered as consisting of three parts of which the most anterior only has the usual relations. This arises by six or seven digitations from the first seven thoracic vertebrae, and passes to a strong tendon that inserts upon the most posterior part of the tuberosity of the humerus. Its tendon is joined by that of a narrow muscle arising from the ridge on the scapula dorsal to the glenoid cavity. This latter muscle is of doubtful homology, and is found likewise in the Echidna where, however, it originates instead "from the posterior extremity of the vertebral margin of the scapula." Mivart calls it a *dorso-epitrochlear* (?), or possibly a separate portion of the *teres major*. Westling (1889, p. 14), however, considers it a part of the *latissimus dorsi* that is not homologous with any separate muscle in other animals. In support of

this view is the fact that a similar division sometimes occurs in man, as pointed out by the same author. If this view be correct, the Echidna furnishes an interesting transition stage between the usual condition in which the *latissimus* is from the vertebral column, and that in the Proechidna in which the supplementary muscle, arising in the Echidna from the vertebral edge of the scapula close to the origin of the main muscle, has instead become shifted about two thirds the distance to the glenoid cavity to take origin from the low ridge at that point. An additional peculiarity of this supplementary portion of the *latissimus* in the Proechidna is that at its origin from the low ridge above the glenoid cavity it becomes split into two. One of the branches is that just described passing to the tendon of the *latissimus*; the second passes laterally as a flat band to its insertion along the ectal margin of the olecranon of the ulna.

The *serratus magnus* is a large muscle, arising from the transverse processes of all but the first of the cervical vertebrae and from strips from each of the four most anterior ribs. It inserts along the vertebral edge of the medial side of the scapula, of which it covers practically the vertebral half. The longest of the digitations is that from the fourth rib, 38 mm. According to Westling, there is a digitation also from the fifth rib in the Echidna.

The *longissimus dorsi* and the *multifidus spinae* are so intimately fused as hardly to be distinguished as separate muscles. The former arises as a thick flat muscle from the head of the ilium and its fibers pass forward to the spines of the lumbar and dorsal vertebrae. The *multifidus spinae* is a series of thin imbricated sheets arising by tendinous fibers from the tips of the transverse processes from the second lumbar vertebra forward. All are closely connected into a single mass that unites the transverse processes to the spines and adjacent parts of the vertebrae, forward including the cervical vertebrae.

What is evidently the homologue of the *iliocostalis* (Plate 1, fig. 1, *ic*) arises by a thin sheet of fascia from the head of the ilium and from the spines of the lumbar vertebrae. It passes obliquely forward as a band some 15 to 20 mm. wide, to about the fifth rib, and on the thorax breaks into a series of short muscular bundles each of which connects the external surface of two adjacent ribs.

The *splenius* takes origin from very thin fascia covering the occiput and the neck as far back as the last cervical vertebra. At the midline the two muscles of opposite sides are continuous.

The *longissimus capitis* is a thicker muscle than the last and arises from the lateral processes of the last four cervical vertebrae. These two muscles have

a common insertion at the mastoid region just dorsal to the external ear and posterior to the insertion of the sternomastoid.

Beneath the *splenius*, and covering the back of the neck is the *biventer cervieis*, a broad muscular sheet, arising from the spines of the first thoracic and all the cervical vertebrae. It inserts by tendinous fibers along the dorsal part of the occiput corresponding to the lambdoid ridges.

The *rectus capitis posterior minor* is quite as large as the preceding and arises from the anterior margin of the atlas, dorsal to the transverse process. According to Fewkes, its origin in the Echidna is from the posterior rim of the atlas. In both it passes forward as a thin sheet to insert upon the posterior part of the occiput, somewhat ventral to the insertion of the *biventer cervieis*.

The *rectus capitis posterior major* was not identified, although it is said to be present in the Echidna as a very small muscle from the anterior extremity of the spinous process of the axis to the occiput.

The *obliquus inferior* originates from the lateral surface of the spine of the axis and passes forward as a strong muscle to insert into the dorsal part of the lateral process of the atlas.

The *obliquus capitis superior* is a short thick muscle, from the ventral side of the transverse process of the atlas to the occiput.

The *rectus capitis lateralis* lies just ventral to the last, and arises from the anterior face of the lateral process of the axis. It passes forward as a stout round muscle to insert just lateral to the insertion of the *obliquus superior*. Mivart states that in the Echidna this muscle has the usual relations, *i. e.*, from the atlas to the occiput, but in the Proechidna its origin is certainly from the axis.

The *longus capitis* arises from the ventral side of the transverse processes of the sixth and seventh cervical and first dorsal vertebrae. It passes forward along the side of the neck as a ribbon-like band, that becomes a flat tendon at the region of the axis and inserts into the jugular process of the skull, just posterior to the tympanic bone.

The *scalenus* is similar to that of the Echidna, arising from the transverse process of the second to seventh cervical, and inserting on the first rib.

**CAUDAL MUSCLES.** — The dorsal muscles of the tail are so intimately connected that they are with difficulty separated into distinct bundles.

The portion corresponding to the *extensor caudae medialis* is of muscle fibers from the spines and dorsal surfaces of the last two lumbar and the succeeding vertebrae, and from the medial edge of the ilium; from this muscle mass, tendons pass to the articulating processes of the vertebrae.

More laterally, fibers arise from the articulating processes of the sacral vertebrae, and from the posterior part of the ilium and lateral part of the vertebrae. These fibers become partly tendinous as they pass dorsocaudal to insert on the dorsal parts of the posterior caudal vertebrae. This muscle is the *extensor caudae lateralis*.

Other and more numerous fibers arise similarly from the posterior margin of the ilium and the dorsal parts of the vertebrae ventral to the articulating processes. The muscle-mass thus formed appears to correspond in part to the *abductor caudae externus*. It passes back along the dorsolateral side of the tail and sends tendons to the anterior margins of the transverse processes of the vertebrae.

The ventral musculature of the tail consists of two main masses, a lateral and a medial, on each side. The former is from muscle fibers arising from the posterodorsal part of the ischium and from the ventral side of the caudal vertebrae adjacent. It forms a tapering bundle inserting by tendinous fibers into the ventral part of the transverse processes. It is probably the homologue of the *coccygeus*.

The more medial masses of muscles arise along the length of the sacral and caudal vertebrae on either side of the median line as a series of bundles that taper posteriorly. They insert by muscle fibers on the ventral part of the coccygeal vertebrae and by strong short tendons that pass to each of the chevron bones. This muscle-mass is probably homologous with the *flexor caudae longus* and the *flexor caudae brevis*.

From the transverse process of the third caudal vertebra a narrow band of muscle passes ventrally, beneath the rectum to join a similar muscle from the opposite side. They together form a muscle that probably corresponds to the *levator ani*. A few muscular fibers join this muscle to the preceding.

MUSCLES OF THORAX AND ABDOMEN.—The *sternomastoideus* originates by muscular and tendinous fibers from the midventral part of the broad lobe of the episternum. Proximally the muscle is flat and broad (about 20 mm. transversely) and is united by fascia to the corresponding muscle of the opposite side. It tapers as it passes forward to its insertion by a stout tendon at the mastoid region, just above the ear.

The pectoral muscles are essentially as in the Echidna. The *ectopectoralis* arises from the side of the manubrium beneath the origin of the *sternomastoideus*, and inserts by tendon on the pectoral ridge of the humerus. A second portion, corresponding to an *entopectoralis* is rather clearly distinguishable, arising

medially from the manubrium to the large third sternum. Its fibers pass likewise in a stout bundle to an insertion on the pectoral ridge of the humerus, slightly posterior and lateral to the insertion of the *ectopectoralis*. In the Echidna the separation of the *ectopectoralis* from *entopectoralis* seems much less clearly marked, if indeed, it is to be distinguished at all. A third portion seems to represent a *xiphihumeralis*. It arises as a narrow muscle at the median line, from the xiphisternum, whence it extends posteriorly about 25 mm. It passes obliquely forward and inserts on the pectoral ridge at the caudal end of the greater tuberosity of the humerus.

In addition to these, there is a large muscle that arises along the entire anteroventral edge of the clavicle from the articulation with the scapula nearly to the median line. Its insertion is likewise on the pectoral crest continuous with and slightly anterior to that of the *entopectoralis*. This muscle both Mivart and Westling find in the Echidna. The former considers it a part of the deltoid on account of its proximity to the acromion at the dorsal point of origin. This interpretation is accepted with some misgiving by Westling, who suggests that it may almost equally well represent a *clavopectoralis*, a view that seems quite as probable.

The abdominal muscles present no special peculiarities, but are essentially similar to those of the Echidna. The *rectus abdominis* is a strong band of muscle fibers some 20 mm. wide, from the base of the epipubic bone passing forward on each side to insert on the ventral prominence of the coracoid and on the ventral half of the first rib.

The *obliquus externus* is strongly developed, and overlies the posterior half or more of the preceding muscle. It arises from the anterior edge of the pubis and the epipubic bone, the tuberosity of the ilium and the lumbar vertebrae, and by a series of muscle strips from the second to the last rib. Each of these strips arises just proximal to the union with the sternal portion of the rib and hence the origins become successively higher dorsally, in passing posteriorly. These strips are all united by fasciae, and between the pubis and the thoracic basket the muscle forms a continuous sheet of fibers, that becomes thickest over the abdomen and is joined as usual to the corresponding muscle of the opposite side.

The *obliquus internus* is in intimate connection with the fibers of the *transversus abdominis* from which it is hardly to be separated. The latter is likewise closely connected with the *obliquus externus* along the lumbar and pelvic origin.

It extends forward along the margin of the thoracic basket to the well-defined *linea alba* at the midventral line.

MUSCLES OF THROAT AND LARYNX.—Fewkes is apparently right in supposing that Mivart has confounded the *sternoglossus* with the *sternohyoideus* and *sternothyroideus* in his account of these muscles in the Echidna. It is the most conspicuous of the throat muscles, and forms a stout round bundle on each side of the pharynx. It arises from the dorsal side of the xiphisternum and passes to the base of the tongue at the upper part of the pharynx, sending a few fibers to the *stylohyoideus* as it crosses the larynx. As shown by Fewkes in the case of the Echidna this muscle can be separated into two portions to which he gives names. In addition, there is in the Proechidna a small thin muscular band at about 25 mm. from the anterior end of the *sternoglossus* on its dorsal side, that passes posterodorsally some 30 mm. to the pharyngeal wall.

What appears to be a *sternohyoideus* arises in the Proechidna mainly from the dorsal side of the manubrium. It forms a single median muscle and inserts into the posterior end of the body of the hyoid. Westling attempts to homologize the *sternoglossus* of the Echidna with the *sternohyoideus* of other animals. Neither this author nor Fewkes mentions the median muscle here considered the *sternohyoideus*, nor is it clear that this muscle is present in a similar manner in the Echidna.

The *sternothyroideus* of the Proechidna likewise presents a few points of difference in comparison with that of the Echidna. It arises from the anterior dorsal edge of the manubrium instead of from the entire dorsal surface of the sternum. It passes forward as a thin band closely applied to the ventral surface of the *sternoglossus*. About halfway on its length it becomes tendinous and receives a short slip of muscle from the side of the *sternohyoideus*. Continuing forward, it again becomes muscular and inserts into the side of the thyroid cartilage.

The *omohyoideus* is present as in the Echidna. It arises at the antero-internal edge of the middle portion of the scapula and tapers to its insertion at the anteroventral border of the thyroid.

The *stylohyoideus* is similar to that of the Echidna, arising from the jugular process just behind the ear. It expands greatly in passing back to its insertion at the midline of the larynx where it is joined by a raphe to the corresponding muscle of the opposite side.

The *geniohyoideus* is a rather narrow muscle from the symphysis to the anterior end of the larynx, where it expands to a width of some 15 mm. It is

largely hidden by the *mylohyoideus*, a thin muscular sheet from the posterior portion of the ramus, beginning some 15 mm. behind the symphysis. The two sheets of opposite sides unite medially by a raphe and insert at the anterior end of the larynx. The *myloglossus* is exposed by laying back the *mylohyoideus*. It is attached on the ventral side of the skull from near the base of the ear on its medial side, forward to the angle of the jaw. It joins the opposite muscle at the midline.

MUSCLES OF THE FORE LEG.—What appears to represent the *deltoides* is present in both the Echidna and the Proechidna as a narrow band arising for a length of about 15 mm. along the anterior edge of the scapula, and at about the same distance dorsal to the junction of the acromion with the coracoid. It narrows to a round stout tendon, that passes anteriorly to the fore leg to its insertion on the anterior side of the tuberosity of the humerus underneath the insertion of the pectoral muscles. This muscle is what Mivart considers a second portion of the deltoid, whose main division he regards as the muscle from the clavicle to the pectoral ridge of the humerus. As already noted, the homology of this larger muscle is somewhat doubtful. From the fact, however, that in the Proechidna, its origin is wholly from the clavicle and its insertion is continuous with those of the other muscles of the *pectoralis* group, it seems better to consider it a *clarpectoralis*.

Owing to the fact that in monotremes the anterior edge of the scapula corresponds to the scapula spine of other mammals, the relations of the muscles in this region differ accordingly.

The *supraspinatus* arises from the entire medial surface of the scapula below the insertion of the *serratus*. It passes out beneath the acromion and episternum and inserts on the anterolateral extremity of the greater tuberosity of the humerus.

The *infraspinatus* takes origin from the ectal side of the scapula, from the anterodorsal angle to the acromion and nearly to the glenoid cavity. It inserts on the greater tuberosity of the humerus just posterior to the insertion of the *supraspinatus* and continuous with it. The condition of these muscles in the Echidna is quite similar.

The *subscapularis* occupies the entire posterior half of the ectal side of the scapula from the vertebral edge, posterior to the ridge above the glenoid cavity. It becomes tendinous and passes to the extremity of the lesser tuberosity of the humerus. From the ridge between it and the *infraspinatus* comes the long head of the triceps. Westling has described in the Echidna a sub-

*scapularis accessorius* which is present likewise in the Proechidna. The origin is directly over the center of the glenoid cavity. It passes ventral to the *triceps* back to the lesser tuberosity of the humerus where it inserts just distal to the insertion of the *subscapularis*.

The *teres major* is a large flattened muscle arising from the extreme postero-dorsal angle of the scapula on the external side. It inserts on the humerus by a broad tendon slightly distal to the insertion of the *subscapularis*.

The *teres minor* is lacking in both the Echidna and the Proechidna. The small muscle described as *subscapularis accessorius* can hardly represent this muscle, on account of its insertion into the lesser instead of the greater tuberosity. According to Sabatier it is fused with the *infraspinatus* which seems extremely probable, since the latter is intimately connected along the anterior edge of the scapula, with the *supraspinatus* where the latter passes out beneath the episternum.

The *coracobrachialis* presents quite the same divisions as in the Echidna. The most superficial is the *caput longum* from the posterior tuberosity of the coracoid by a broad tendon. It passes as a broad muscular band to the internal distal condyle of the humerus where it is inserted by short tendinous fibers. Underneath this head, and from the same origin is the *caput breve*, which spreads out as a thin muscular sheet over the posterior aspect of the head of the humerus from the lesser tuberosity to the center of the depression between the two tuberosities, and distally for nearly three fourths the length of the humerus. The third portion is much smaller, and is wholly overlaid by the second head. It arises slightly anterior to the latter, in part from the lateral surface of the epicoracoid and passes as a short tenuous sheet to insert on the lesser tuberosity of the humerus just posterior to the insertion of *subscapularis*. This is the *epicoracobrachialis* of Coues.

The *biceps* arises from the ventral surface of the coracoid below the glenoid cavity. At its anterior edge may be separated off a small slip whose origin is from the epicoracoid. The two are closely approximated and after about 20 mm. become inseparably fused to form a stout muscle that passes to a tendinous insertion nearly a centimeter in length on the medial side of the radius, nearly the same distance distal from the sigmoid cavity. The same condition, essentially, is found in the Echidna in which the small slip from the epicoracoid is considered by Westling a second head. The action of the muscle is to approximate the fore arm to the breast.

The *triceps* is very strongly developed, and is separable into the usual

three divisions. The *caput longum* has origin by a short stout tendon just dorsal to the glenoid cavity of the scapula, at the ventral end of a small ridge. In the Echidna this origin is much more extensive, and is represented as continuing dorsally almost to the vertebral edge of the scapula. Also the deltoid and the small branch of the *latissimus dorsi*, previously noticed, are in the Echidna from nearer the vertebral edge, since their origin is slightly dorsal to that of the *caput longum*. The insertion of this muscle is as usual into the tip of the olecranon. The *caput laterale* arises by a stout tendon from the lateral face of the humerus at nearly the end of its proximal third. It inserts at the external corner of the olecranon, and is fused distally with the *caput mediale*. This last covers the entire posterior aspect of the humerus, from just below the head, to the deltoid ridge and inserts into the middle and medial borders of the olecranon beneath the *caput longum*.

The *brachialis* in the Proechidna is almost inseparable from the *brachioradialis*, along the medial side of which it is so closely applied as to be with difficulty separated. Its origin is just lateral to the anterior edge of the humerus at about the end of its proximal third. It passes to the ulna, on whose medial side it is inserted by a thin tendinous sheet just anterior to the sigmoid notch.

The *anconeus* (Plate 1, fig. 3, *an*) is a well-defined band some 30 mm. long that arises at the external border of the posterior distal tubercle of the humerus and passes anteriorly to the olecranon of the ulna where it inserts just posterior to the *caput mediale* of the *triceps*.

The *brachioradialis* is similar to that of the Echidna. It arises on the external side of the humerus, distal to the tendon of origin of the *caput laterale* of the *triceps*, and occupies nearly the middle third of the humerus. It passes as a thin sheet to a partly tendinous insertion along the medioventral border of the radius for some 25 mm. distal to the sigmoid notch. Its internal surface is very closely connected with the *brachialis*, which, however, is of about half the extent of the *brachioradialis* along the line of insertion.

The *extensor carpi radialis longus* (Plate 1, fig. 2, *erl*) is a narrow muscle, somewhat triangular in section, that arises from the lateral supracondyloid ridge of the humerus, just distal to the *brachioradialis*. Slightly beyond the middle of the radius it passes into a flat tendon that runs over the distal head of the radius and inserts upon the dorsal surface of the combined *radiale* and *intermedium* ("seapholunar bone").

The *extensor carpi radialis brevis* (Plate 1, fig. 2, *erb*) is of nearly four times the bulk of the *longus* and arises just external to it from the supracondyloid

ridge. It becomes tendinous at a point slightly more distal than the *longus*, and the tendons of both muscles pass together beneath the tendon of the *extensor brevis pollicis*, and along a slight groove on the distal head of the radius. The tendon of the *brevis* division becomes very flat and inserts on the dorsal side of the third metacarpal at its proximal end. The condition of these two muscles is thus quite the same as in the Echidna.

The *extensor digitorum communis* (Plate 1, fig. 2, *ed*) is likewise practically identical with that of the Echidna. It arises from two heads:—(1) a narrow muscular strip from the extreme anterolateral border of the external epicondylus and (2) a deeper muscle overlaid by the *extensor digitorum lateralis* and *extensor carpi ulnaris*. It arises along the proximal two thirds of the anterolateral border of the ulna medially to the line of contact with the radius from which also come a few fibers. Both heads unite at about two thirds the length of the fore arm and pass as a flat tendon along the depression between ulna and radius. On the carpus, the tendon divides into three branches, one each to the dorsal margin of the distal phalanx of digits 2, 3, and 4. In the Echidna, notwithstanding that the fifth digit is clawed and hence more functional as a digging organ than the clawless knob representing that digit in the Proechidna, the *communis* tendons are likewise three, one each to the same digits, although a fourth branch to digit 5 might have been expected.

The *extensor digitorum lateralis* (Plate 1, fig. 2, *el*) is a very thin narrow band arising by a flat tendon from the lateral epicondylus of the humerus and from the under side of the *extensor carpi ulnaris*, for about 6 mm. out from its proximal end. It is thus largely covered by this muscle and its flat tendon appears just proximal to the wrist, and passing over the hand, inserts at the proximal end of the terminal phalanx of digit 4, underneath the lateral branch of the *communis* tendon. In the Echidna the condition is quite similar.

The *extensor carpi ulnaris* (Plate 1, fig. 2, *eu*) is a flat muscle from a broad origin by tendinous fibers extending between the distal edge of the lateral epicondylus of the humerus to the dorsal edge of the base of the ulna. The muscle tapers to a strong round tendon that passes over the distal head of the ulna where it runs along a shallow groove to the outer edge of the hand and inserts as in the Echidna into the first phalanx of the fifth digit at the proximal end.

The *supinator* is a stout muscle, triangular in cross section, lying under cover of the *extensores carpi radialis et ulnaris*. It is inserted along the anterior surface of the proximal half of the radius.

The *extensor brevis pollicis* (Plate 1, fig. 2, *ep*) is essentially as described

for the Echidna, arising by tendinous fibers from the median edge of the ulna just distal to the sigmoid notch and by fibers from the ligament between ulna and radius. Proximally the muscle is closely applied to the *supinator*, and then passes as a stout flattened tendon across the tendons of the *extensores carpi radialis longus et brevis* to insert on the radial side of the first metacarpal.

The *pronator teres* (Plate 1, fig. 2, *pt*; fig. 3, *pt*) is strongly developed. It has origin by a flat tendon from the medial edge of the internal epicondylus of the humerus and is partly covered by the *flexor carpi radialis*. The muscle thickens in the middle, and becomes somewhat triangular in section. Distally it flattens again and inserts by muscular fibers along the medial edge of the radius from the insertion of the *biceps* to the epiphysis.

The *flexor carpi radialis* (Plate 1, fig. 3, *fr*) is a large, radially compressed muscle, arising from the anterior edge of the internal epicondylus of the humerus slightly external to the origin of the *pronator teres*, whose base it slightly overlaps. It passes into a stout tendon at the beginning of the terminal third of the fore arm and inserts into the proximal end of the second metacarpal, ventrally, and by a continuation of the tendinous portion it is likewise united with the first metacarpal. The condition is essentially the same as in the Echidna.

The *palmaris longus* is lacking, at least as a separate muscle. Mivart considers that it is fused in the Echidna with the *flexor profundus digitorum*.

The *flexor carpi ulnaris* (Plate 1, fig. 3, *fu*) is from two heads as usual:— (1) for nearly one third the length of the ulna from the olecranon along its ectal edge, (2) by a smaller flatter muscle arising at the ectal corner of the epicondyle of the humerus, where it partly overlies the most exterior head of the *profundus*. The ulnar head is the larger and the tendons of the two unite just proximal to the distal head of the ulna and insert as usual into the pisiform bone. Proximally the second head is united by a few fleshy fibers to the base of the *profundus*.

The *flexor sublimis digitorum* is lacking as a separate muscle.

The *flexor profundus digitorum* (Plate 1, fig. 1, *p*; fig. 3, *p*) is enormously developed and arises from four heads:— (1) an ulnar head, from the proximal two thirds of the inferior surface of the ulna and from fascia between the radius and ulna; (2) from the angle of the internal epicondylus of the humerus where it is partly covered by the second head of *flexor carpi ulnaris*; (3) a thick portion arising also from the internal epicondylus, just medial to the second portion of the *profundus*, to which it is intimately connected by muscular and tendinous fibers; (4) a deep lying slender and spindle-shaped muscle quite distinct from

the other heads and completely covered by them, which arises from the ectal border of the internal epicondylus under head 2 and passes into a tendon which unites with the main tendon at the wrist. The large common tendon covers the palm and at the base of the metacarpals divides into three strong flat tendons, one each to digits 2, 3, and 4. Each tendon runs along the inferior side of its digit, and just distal to the base of the metacarpal passes through a transverse loop. It inserts in the terminal phalanx of the digit. This muscle in the Echidna differs remarkably in that there are five divisions of the great tendon, one each to the five claws. According to Mivart each tendon likewise passes through a cross-loop at the metacarpal, except that of the pollex, but Fewkes found that division as well passed through a loop. In the Proechidna, therefore, the division into three instead of five tendons is correlated with the reduction of the clawed digits to three, showing that this difference is of a somewhat profound character, functional as well as anatomical, for there is no trace of the two lost branches to the now reduced first and fifth digits in the Proechidna. In all other respects, however, the muscles of the fore limb are essentially alike in the two animals. It would be interesting to know the condition of this muscle in the occasional specimens of the Proechidna with more than three claws.

The *lumbricales* are four in number arising from the great pad of the *profundus* tendon; the two muscles of the first pair pass distally to the fascia surrounding metacarpals 2 and 3 respectively, those of the second pair pass in like manner to the approximated sides of metacarpals 3 and 4. The two middle muscles of these four are practically fused into a single mass.

From the dorsal (carpal) side of the pad of the *profundus* arise three other small and flattened muscles:— the first originates between the tendons to digits 2 and 3 and passes to the fascia between those digits; the second takes origin from between the tendons to digits 3 and 4 and in like manner passes to the fascia between them; the third muscle arises slightly external to the base of the tendon of digit 4, and goes to the fascia between digits 4 and 5.

There are in addition seven other small muscles in the deeper portion of the hand. Three of these arise from the tendinous insertion of the *flexor carpi radialis*, the most external of which passes to the end of the first digit on the radial side. It is very probably the homologue of the *adductor pollicis* (Plate 1, fig. 3, *ap*) and is present likewise in Echidna. The two other small muscles pass one to the radial and one to the ulnar side of the second digit and insert on its first phalanx. In a similar fashion, two other small muscles

arise at the base of the third metacarpal and pass one to its radial and one to its ulnar side, inserting on the first phalanx. From a similar origin in the fascia covering the carpals at the base of the fourth metacarpal a small muscle passes to the investing tissue on the radial side of metacarpal 4, but there is no corresponding muscle on the ulnar side, unless, as seems quite probable, this is represented by a small muscle passing to the radial side of the *fifth* digit, that takes origin from a cartilaginous pad running from the pisiform bone to the base of digit 4. These five small muscles are doubtless to be considered the *interossei* (Plate 1, fig. 3).

A seventh small muscle arises just distal to the pisiform bone in the anterior prolongation of the tendon of *flexor carpi ulnaris*, and passes to the radial side of digit 5, into the terminal phalanx of which it inserts. This muscle seems to correspond to an *abductor digiti quinti* (Plate 1, fig. 3, *ab*). This last muscle apparently is not present in the Echidna, as it was not found by Mivart, Fewkes, or Westling. It is possible that it has been retained in the Proechidna to counterbalance the loss of the tendon from the *profundus*, as otherwise the fifth digit would be unprovided with a special flexor. The interossei of the Proechidna seem to be essentially as in the Echidna.

MUSCLES OF THE HIND LEG.—Concerning the homology of the *glutei* (Plate 1, fig. 1, *gm*, *gme*) in the Echidna, there has been more or less disagreement, and their relations in the Proechidna are quite similar. That portion of the *panniculus* muscle from the spines of the coccygeal vertebrae to the fascia investing the tibia (named by Fewkes the *dermo-flexor cruris*) was considered by Mivart a *gluteus maximus*. This muscle is also present in the Proechidna, as well as a second muscle just anterior, whose counterpart is found in the Echidna. In the former animal this second muscle is a broad sheet arising by thin aponeurosis from the third and fourth sacral and first caudal vertebrae. It tapers to an insertion by a flat tendon at the middle of the femur along the distal end of the trochanteric ridge. This muscle Mivart is inclined to consider a *gluteus medius* and Westling follows this determination. Fewkes doubts Mivart's interpretation, and would call this muscle a *glutus maximus*, at the same time giving a new name to the superficial muscle to which Mivart had assigned the term *maximus*. From its origin and insertion there can be but little doubt that Fewkes is correct, but it is further probable that the cutaneous muscle (*dermo-flexor cruris*) may be a derivative of the *gluteus maximus*, as indeed Mivart suggested. The two divisions therefore would be analogous to the cutaneous and brachial portions of the *latissimus dorsi*.

What is clearly the *gluteus medius* (Plate 1, fig. 1, *gme*) is present in much the usual relations. It is a large muscle-mass arising from the lateral face of the ilium, and from fascia connecting the spines of the last lumbar and first two sacral vertebrae. It inserts on the head of the femur from the great trochanter to the acetabulum. What seems also to be a division of this muscle arises from the lateral part of the tuberosity of the ilium and passes as a rather easily separable bundle to an insertion about 10 mm. long at the proximal end of the trochanteric ridge. The muscle here considered the *gluteus medius*, Mivart and Westling have taken to be the *minimus*, since they assigned to the *medius* the crural division of the *maximus*. The *minimus* is, however, wanting as a distinct muscle in both the Echidna and the Proechidna.

The *pyriformis* (Plate 1, fig. 1, *py*) seems to be represented by a small muscle from the tips of the transverse processes of the fourth sacral and first caudal vertebrae. It passes over the posterior tuberosity of the femoral head and inserts on the lateral side of the trochanteric ridge at slightly less than half its length, just caudal to the insertion of the *gluteus maximus*. Between the latter and the *pyriformis* issues the sciatic nerve. Mivart found a similar muscle in the Echidna arising from five caudal vertebrae, but Westling failed to find it. Mivart notes that the nerve is superficial to the muscle instead of beneath it as usually.

The *capsularis* shows the usual relations. It arises as a thin sheet from the ilium between the acetabulum and the origin of *rectus femoris* and spreads out to an insertion about 10 mm. long at the proximal portion of the trochanteric ridge.

The *quadratus femoris* is a large muscle from a triangular origin extending from the tuberosity of the ischium to the acetabulum. It is inserted by tendinous fibers on the great trochanter just distal to the insertion of the *gluteus medius* and for about 10 mm. along the trochanteric ridge. Mivart speaks of this as a "delicate" muscle in the Echidna.

The *obturator externus* appears to be much as in the Echidna. It is large, of a triangular outline, and lies as usual underneath the *adductor femoris*. It originates from the anterior edge of the pubis at the base of the epipubic bones, and thence along the entire pubic symphysis and for about 15 mm. on the ramus of the ischium. At the most anterior portion the origin extends from the pubic border to the lip of the obturator foramen, but elsewhere it is from the outer edge of the pubis and ischium, whence it tapers slightly to the insertion in the entire intertrochanteric fossa.

The *obturator internus* is wanting as in the Echidna.

The *iliopsoas* is a large mass from two heads:—(1) the *iliac* portion which arises from the ventral side of the ilium from its tuberosity nearly half way to the acetabular notch; (2) the *psoas* portion from the three last lumbar vertebrae. The common insertion is by muscular and tendinous fibers into the lesser trochanter for about one half the distance between the lesser trochanteric head and the distal epiphysis of the femur. In the Echidna the *psoas* portion has origin from the three last lumbars and first sacral, but in the Proechidna the origin seems to be from the lumbars only.

The *psoas minor* arises from three heads, one each from the two last dorsal and the first lumbar vertebrae. The most anterior of these heads extends laterally on to the proximal end of the rib. The muscle narrows to a powerful tendon that inserts as usual on the anterior edge of the pubis directly in front of the acetabulum. In the Echidna the origin is slightly different, according to Mivart, “from the last three ribs, and . . . the bodies of the last three dorsal vertebrae.” This difference may be correlated with the presence of an additional lumbar in the Proechidna.

The *biceps femoris* (Plate 1, fig. 1, *bf*) as in the Echidna, arises from a single head, by stout tendon from the lateral portion of the ischial tuberosity. It forms a flat sheet of muscle, triangular in outline and is broadly inserted along the lateral margin of the proximal three fourths of the tibia into the sheet of fascia investing the lower leg, and by a thin tendinous sheet continuous with this, into the lateral margin of the patella.

The *semitendinosus* (Plate 2, fig. 4, *st*) is from the lateral edge of the ischial tuberosity, a broad flattened band, inserting by muscular and tendinous fibers on the medial border of the tibia underneath the insertion of the *gracilis*.

The *semimembranosus* (Plate 2, fig. 4, *sm*) is a somewhat similar broad muscle, arising by tendinous fibers directly underneath the origin of the *semitendinosus*, on the tuberosity of the ischium. It inserts by a stout tendon on the medial surface of the head of the tibia.

The *sartorius* (Plate 2, fig. 4, *sa*) takes origin as a flat thin band for about 10 mm. along the anterior edge of the pubis just dorsal to the epipubic bone. It passes to the fascia investing the knee at the medial border of the distal head of the femur and the proximal head of the tibia.

The *gracilis* (Plate 2, fig. 4, *g*) muscles of opposite sides are separate medially. Each arises as a broad flat muscle from the basal one sixth of the epipubic bone, the entire pubic symphysis, and for a short distance on the ramus of the ischium. It inserts on the medial face of the tibia at the beginning of its second fourth.

The *adductor femoris* (Plate 2, fig. 4, *af*) has the usual two heads, *magnus* and *brevis*. The former arises along the caudal margin of the ischium, in part covered by the *semimembranosus*, from the tuberosity for slightly more than half the distance to the posterior end of the symphysis pubis. It inserts partly along the medial and posterior side of the distal end of the shaft of the femur, and in part by tendon in common with the *brevis* division on the medial epicondyle of the femur under cover of the *sartorius*. The *brevis* division arises along the symphysis pubis under cover of the *gracilis*. Its insertion is in part by the common tendon and thence proximally on the middle third of the femur.

The *adductor longus* (Plate 2, fig. 4, *al*) is wanting in the Echidna, but in the Proechidna seems to be represented by a short compressed muscle arising from the external base of the epipubis. It is inserted along the medial edge of the distal third of the femur in close association with the *pectineus*.

The *pectineus* (Plate 2, fig. 4, *pec*) is a somewhat similar muscle arising just dorsal to the *adductor longus*, on the anterior edge of the pubis. Its insertion is in close approximation with that of the latter, on the medial edge of the femur, but is slightly shorter.

The *rectus femoris* (Plate 2, fig. 4, *rf*) is from the ilium just anterior to the acetabulum and passes to its insertion into the proximal border of the patella and the fascia ensheathing the knee.

The *vastus lateralis* arises by muscular fibers from the whole anterolateral side of the femur from the median line to the trochanteric ridge. It inserts upon the lateral edge of the patella and becomes fused distally with the *rectus femoris* and *vastus medialis*.

The *vastus medialis* (Plate 2, fig. 4, *va*) is slightly smaller than the *lateralis*, and takes origin from the anteromedial portion of the shaft of the femur. It is partly fused with the two preceding muscles distally and inserts also on the medial side of the patella. A *vastus intermedius* is not to be distinguished in either the Proechidna or the Echidna.

The muscles of the lower leg are weak and slender. The *gastrocnemius* (Plate 2, fig. 4, *gas*) has much the same relations as in the Echidna. There is but a single head, from the ventral side of the medial tubercle of the femur, a flat narrow muscle that passes into a flat tendon on the lower half of the leg, and is inserted into the calcaneum at its external border.

The *soleus* (Plate 2, fig. 4, *so*) is a similarly shaped muscle, arising from the external side of the ascending proximal end of the fibula. Its tendon becomes bound by connective tissue to that of the *gastrocnemius*, and the two pass side

by side to the tarsus, where the *soleus* tendon passes underneath that of the latter to insert on the calcaneum.

Just medial of the origin of the *soleus*, at the tip of the fibular process arises a short flat muscle which passing into a long tendon, crosses under the *gastro-enemius* to the medial side of the leg, and passing through the groove between the distal head of the tibia and the naviculare, inserts at the base of the terminal phalanx of the first digit. It is also connected with the general fascia of the sole of the foot. This muscle is present in a similar relation in the Echidna, and is considered the homologue of the *plantaris* (Plate 2, fig. 4, *pla*) by Mivart and by Westling, an interpretation which is probably correct notwithstanding that there is no femoral origin, and that the insertion (at least in the Proechidna) is definitely into digit 1.

The *popliteus* does not originate from the femur but from fascia between it and the long proximal extension of the fibula, and mainly by muscular fibers from the medial surface of this part of the fibula itself. It passes as a thick triangular muscle to an insertion on the medial edge and ventral part of the tibia for a centimeter or more at the proximal end. The same conditions obtain in the Echidna.

Partly underneath the origin of the *soleus* and extending slightly external to it on the head of the fibula arises the chief flexor of the foot, which appears to correspond to the *flexor longus digitorum* (Plate 2, fig. 4, *fld*). The origin is by tendinous fibers from slightly more than the proximal half of the postero-external aspect of the fibula. At the tarsus it becomes a stout tendon that inserts upon the internal edge of the calcaneum and then spreads out in the broad plantar fascia of the foot. Its four main tendons go to digits 1, 2, 3, and 4 respectively, inserting into the terminal phalanx. A fifth tendon comes off from the plantar pad between the tendons to the first and second digits and passes to the basal phalanx of the second digit on the external side. A similar tendon comes from between those to the second and third digits, and inserts on the basal phalanx of the third digit, making thus six tendons from the plantar pad. There appears to be no branch to the fifth digit.

Wedged in between the heads of the *soleus* and the *plantaris* and covered by them is a very small compressed muscle arising from the lateral margin of the proximal end of the fibula. At about half way on the length of the tibia it becomes a small tendon that joins the ental margin of the great tendon of the *flexor longus digitorum*, just proximal to the tarsus. This tendon is not traceable farther as it is fused with that of the latter muscle. This muscle

probably represents the *flexor longus hallucis*, and possibly gives rise to some of the small tendons described in connection with the *longus digitorum* as going to the bases of digits 2 and 3.

In the Echidna, the condition described for the flexors is quite different. There are five tendons described by Mivart, from the *flexor longus digitorum*, one to each of the five phalanges, and no *flexor longus hallucis*. Westling and Cunningham, however, found but four tendons from the *longus digitorum*, one each to digits 1 to 4. The small *longus hallucis* was not found in the Echidna by Mivart or Westling, nor does either mention the two additional small tendons from the plantar pad to digits 2 and 3, that are present in the Proechidna, apparently as parts of the *flexor longus hallucis*.

Three small muscles representing the *lumbricales* arise from the inferior side of the plantar pad and pass to the bases of the second to fourth digits respectively as small tendons. On the dorsal side of the plantar pad three other small muscles arise and pass to the third, fourth, and fifth digits respectively, on their external sides.

The *tibialis posterior* is a large muscle, nearly the size of the *flexor longus digitorum*. It arises from the proximal three fifths of the lateral and posterior sides of the fibula and from aponeurosis between tibia and fibula. It is covered in part by the heads of the *soleus*, *plantaris*, and *flexor longus*, and passes to a stout tendon running in the groove between the tibia and fibula just medial to the spur, and inserts into the proximal end of the astragalus. The condition in the Echidna is quite the same.

The *peroneus longus* (Plate 1, fig. 1, *pl*) is the most lateral of the lower leg muscles. It originates on the external side of the head of the fibula for about 15 mm. beginning just below the tip of the proximal extension. It tapers to a stout flat tendon as it reaches the end of the shaft, passes over the epiphysis of the fibula, and thence through the groove on the peroneal tubercle of the calcaneum, after which it goes to the ventral side of the foot to its insertion on the proximal edge of the fifth metatarsal; a small branch from the inserting tendon crosses the foot to the basal phalanx of the first digit. In the Echidna the condition seems to be much the same, although neither Mivart nor Westling mentions the insertion of the tendon into the fifth metatarsal, which is a prominent feature in the Proechidna.

The remaining *extensores* of the hind foot are essentially the same as in the Echidna although apparently differing in a few slight details. The homology of these muscles is not altogether certain.

Next internal to the muscle last described arises what is doubtless the *extensor longus digitorum* (Plate 1, fig. 1, *el*). Its origin is from a flat broad tendon from the outer epicondyle of the femur, between the ascending process of the fibula and the patella. It passes to the inner tubercle of the fibula on which it is inserted and thence into a large flattish muscle that arises from the proximal half or more of the fibula, and (medially) from the interosseous fibers between tibia and fibula. This muscle is easily divisible into three parts:— the most external comes off superficially from the main muscular mass at 20 mm. below the head of the fibula and continues as a small spindle-shaped muscle to the distal head of the fibula where it passes into a delicate tendon that inserts as a thin sheet at the base of the fifth digit. In the Echidna Mivart found this branch inserting on the fourth digit of the *left* leg, but on the fifth digit of the *right* leg. He considers it a part of the *flexor longus digitorum*. Westling also in the Echidna, found a similar branch, whose tendon, however, became divided into two, the outer to the fifth, the inner to the fourth digit. This author considers the outer branch the equivalent of the *peroncus brevis*, and names the muscle *extensor digitorum IV et V*. From the condition in the Proechidna, however, it seems better to consider this muscle as representing a branch to the fifth digit from the *extensor longus digitorum* that, on account of the reduction of the fifth digit, is in process of becoming quite separated. The branch to the fourth digit noted by Westling may be due to an imperfect separation of the fourth digit's tendon, since the small muscle is very closely appressed against the edge of the *extensor longus*.

The main portion of the *extensor longus* is radially compressed, but becomes flattened as it passes through the groove between the distal heads of tibia and fibula. On the tarsus it spreads out as a thin sheet of fascia to the bases of digits 2, 3, and 4. This sheet is continuous at the bases of the phalanges with the tendon to the fifth digit above noted.

Closely approximated against the medial border of this main portion, is another muscle nearly as large proximally, but passing at the distal epiphysis into a broad flat tendon. At the metatarsals this tendon becomes dorsal to that of the main tendon of the *longus digitorum* and goes to the bases of the second (mainly) and third phalanges. In the Echidna, the same condition was found by Westling, who names the muscle *extensor digiti II*. Mivart noted only the main insertion, that on the second digit, and considers the muscle equivalent to the *extensor longus hallucis*, even though it has no connection with the hallux. It is possibly a derivative of the *extensor longus digitorum*.

There remain two additional *extensors* at the tibial side of the leg. The more external arises by muscular fibers from between the heads of tibia and fibula, from the interosseous ligament, and mainly from the proximal two thirds of the shaft of the tibia. At the tarsus it becomes a flat tendon passing to the external side of the first digit. Closely applied to this muscle and practically united with it at the origin along the anterior side of the tibia, is a second and broader muscle likewise passing to a tendon that inserts beside the first on the dorsal surface of the hallux. Mivart, who regards both these muscles in the Echidna as parts of the *tibialis anterior* states that the internal tendon passes beneath the external at the insertion, but this is not true in the Proechidna. Probably Westling is correct in considering the more internal of these two muscles the *tibialis anterior* (Plate 1, fig. 1, *ta*) and the more external the *extensor longus hallucis*.

From the foregoing account it is evident that the musculature of the Proechidna is in the main similar to that of the Echidna. The chief points of difference are the following:— the supplementary portion of the *latissimus* arising in the Echidna from the vertebral angle of the scapula, originates instead from the ridge just dorsal to the glenoid cavity, and here sends out a second branch to the olecranon; the *serratus magnus* arises from the four most anterior ribs in the Proechidna, whereas in the Echidna the five anterior ribs are involved; the *rectus capitis lateralis* is from the axis in the Proechidna instead of from the atlas; a single median muscle, apparently a *sternohyoideus* is present, but seems to be lacking in the Echidna; the origin of the *caput longum* of the triceps is short, from the ridge on the scapula just dorsal to the glenoid cavity, whereas in the Echidna the origin extends nearly to the vertebral edge of the scapula; the *flexor profundus digitorum* in the Proechidna sends tendons to digits 2, 3, and 4 only, instead of to all five digits of the hand as in the Echidna; this difference, correlated with the reduction of the clawed digits to three in the former, seems of considerable importance, since the functional loss of digits 1 and 5 is correlated with the disappearance of their respective flexors; in the manus of the Proechidna a muscle apparently representing the *abductor digiti quinti* is present, but seems to be absent in the Echidna; an *adductor longus* of the hind leg seems to be wanting in the latter but is present in the Proechidna; there is also present in the hind leg a small muscle probably representing a *flexor longus hallucis*, whose tendon becomes fused with that of the *flexor longus digitorum*; this muscle is not present in the Echidna.

## VISCERAL ANATOMY.

DIGESTIVE TRACT.—As long ago as 1877, Paul Gervais pointed out that the *tongue* of the Proechidna was much more highly developed than that of the Echidna, in correlation with the greater development of the beak. Its length he gave as 270 mm., while that of the Echidna was but 85. The horny papillae at its base are differently disposed, and its anterior portion which is trough-like is provided with three longitudinal series of spines, one median and two marginal, whereas the tongue of Echidna is smooth save at its base. The tongue of an adult Proechidna in the material studied, is 290 mm. long, of which the three rows of horny points, backwardly directed, occupy the terminal 80 mm. Of these points there are about 20 in the median and 22 in each of the lateral rows. The portion of the tongue bearing these points is flattened, with the margins slightly inrolled. Back from this tip, it is cylindrical and increases to a diameter at its base of nearly 14 mm. There is a patch of scattered horny papillae, backwardly directed, at the very base of the tongue. The tongue of a young individual is but 85 mm. in length and there are only 15 horny papillae discernible in each row at the tip of the tongue.

This young individual shows a series of *palatal papillae* in the midline of the rostrum. These are likewise directed backward, and the largest measure about 2 mm. in length. The first eight are each divided by a median furrow into a right and a left half. In the first six of these each half is secondarily divided into three minute lobes, one anterior and two posterior, but in the two following, the two posterior points are reduced to one. Farther back, the ninth to twelfth are single median papillae, and decrease regularly in size till the last two are almost imperceptible except as small rounded prominences, the last about opposite the middle of the orbit. At the posterior end of the palate are three transverse rows of horny, tooth-like papillae, the first of seven, the second of ten, the third of nine. These rows are about 4 mm. apart. In an adult specimen Gervais (1877-'78) describes five rows of these processes.

I can add nothing to what has previously been published on the *salivary glands* of the Proechidna. Viallanes (1879, 1880) has described the large elongate and flattened submaxillary glands which are very conspicuous in both the Echidna and the Proechidna. The terminal portion of the duct of these glands is larger in the latter, and reaches from the base of the tongue to the symphysis of the lower jaw. It expands into a fusiform reservoir with very glandular

walls, and from the internal face of this reservoir, as traced by injecting, pass four or five secondary canals that open directly on the floor of the mouth. In the Echidna there appears to be no such reservoir but the openings of the duct are more numerous, and lie in a single straight line from the base of the tongue to the symphysis. The same author describes a second part of the submaxillary gland in the Echidna, a superficial glandular mass, a little larger than the parotid, placed immediately under the skin, against the pectoral muscle. Its long duct runs forward to join that of the deeper submaxillary. I was unable to discover any trace of such a duct in the Proechidna. Viallanes also describes parotid glands in the Echidna rather far to the rear of the auditory conduit, and a sublingual gland in both Echidna and Proechidna that opens by a number of ducts into the floor of the mouth. The great development of the salivary glands in these and other ant-eating animals, as Tamandua, and the Golden-winged woodpecker, is doubtless an adaptation, perhaps for neutralizing the large amount of formic acid in the ants on which they feed.

The *stomach* of the specimen dissected is globular, about 70 mm. in transverse by 50 mm. in longitudinal diameter, with the oesophagus and pylorus only about 30 mm. apart. The small intestine measured about 2,450 mm., the large intestine about 480. The caecum (Plate 2, fig. 5) is short and with a rounded compressed tip. Its extreme length is 12 mm., its greatest diameter about 5.5. Its appearance seems almost identical with that of the Echidna.

The *liver* is large and rather thick. The left lateral lobe is rounded and simple, about 50 mm. in diameter and 20 thick. The right lateral lobe is of nearly the same size, but more elliptical in outline. Its cranial lobe is simple, thick, and rounded. Upon it lies the caudal portion which is of about two thirds its bulk and hollowed slightly at the posterior surface to receive the right kidney. The Spigelian lobe is stout and well developed, nearly an equilateral triangle in outline. The median lobe of the liver is the largest. Its cranial surface is undivided but its caudal surface is traversed by a deep furrow that divides it into a left median lobe and a cystic in which the gall bladder is superficially placed. This latter in the young specimen studied, is small and pyriform, about 20 mm. long by 12 in greatest diameter. In an adult animal it is more than twice these dimensions and of an elliptical outline, with the long axis at right angles to that of the body. The bile duct runs into the substance of the pancreas where it receives the short pancreatic duct about 2 cm. before it enters the small intestine at about the same distance from the pylorus.

The *pancreas* itself is flattened and oval, of rather firm consistency, and

lies in a loop of the small intestine. It measured 37 by 16 mm. in the young specimen examined. Its duct is short and as just noted, joins that from the gall bladder within the substance of the pancreas. Chapman (1887) in his account of the anatomy of the Echidna states that the pancreas has a separate duct in the specimen he studied and it enters the intestine at a point nearer the pylorus than does the bile duct. This, as he admits, is contrary to the usual condition, and must have been abnormal.

**MESENTERIES.**—The duodenohepatic ligament is short, about 15 mm. long. About the same distance posteriorly is a short ligament binding the small intestine to the caudate lobe of the liver. The omental sac is largely developed, consisting of a thin and delicate mesentery with deposits of fat along the courses of the blood vessels. The large spleen is bound by it to the cardiac curvature of the stomach. The mesorectum and the mesocolon go forward to the anterior end of the large intestine, at which point the mesentery passes in a fan-shape to the entire length of the small intestine except for a short space, about 15 mm., at a point nearly thrice that distance back from the pylorus.

**SPLEEN.**—The *spleen* (Plate 2, fig. 6) is practically like that of the Echidna, proportionately large and of three distinct lobes:—a long narrow lobe, about 38 mm. long and 11 wide along the edge of the cardiac curve of the stomach, a similar but longer (80 mm. by 10) lobe on the greater or posterior curvature, and third, a lobe lying in the mesentery of the large intestine, narrow at first, but becoming terminally a large rounded mass, about 28 mm. in longest diameter and 19 mm. in transverse diameter.

**KIDNEYS AND GENITALIA.**—The *kidneys* and *genitalia* seem to be quite as in the Echidna. The former are large and rounded, about 32 by 23 mm. in the specimen studied, and 18 mm. thick. The adrenal body lies just anterior to the hilum on the medial side of the kidney, is oval in outline, and measures about 14 by 7.5 mm. The ureters do not empty into the bladder directly, but run each to a point at its mouth just posterior to the opening of the vas deferens. The two ducts open here into the urethra by a common orifice provided with a small papilla. The testis is received into a slight hollow of the body-wall. The penis lies in the floor of the cloaca. As in the Echidna its gland is divided into four lobes. The cloaca is some 25 mm. long, and the large intestine enters well posterior to bladder, ureters, and vasa deferentia.

**LUNGS.**—The *lungs* (Plate 2, fig. 7) seem rather small in proportion to the size of the animal. The right lung has two lobes. The larger extends the entire length of the pleural cavity and enfolds the smaller or ventral lobe so

that in ventral aspect, the latter appears to lie in a transverse depression of the large lobe. The left lung is simple, but has a slight cleft on the ventral margin anteriorly. A large azygos lobe lies transversely just posterior to the heart. Its shape is pyramidal, with a triangular cross section; its base lies near the middle of the right lung and it tapers to a point on the left side, where it is partly received into a depression of the ventral surface of the left lung. Apparently the condition is much the same in the Echidna, though Westling (1889) states that in this animal the right lung is three-lobed, the left single. Apparently the azygos lobe was included with the two lobes of the right lung.

### PLEXUSES.

The plexuses of the Echidna have been studied and carefully figured by Westling (1889) and those of the Proechidna appear to differ but little. The brachial plexus is composed of the same nerve trunks in both animals. In the Proechidna, cervical nerves 7 and 8 unite almost at once to form a common trunk. The fifth and sixth cervicals are about equally large and unite with the combined seventh and eighth at about 17 mm. from the exit. Cervicals 3 and 4 are slightly smaller and the former unites with a very small second cervical before joining the other, chief trunk.

The lumbosacral plexus is formed by nerves from the last dorsal, the four lumbar, and two anterior sacral vertebrae. In the Echidna, Westling figures this plexus from an animal having 15 and another having 16 dorsal vertebrae. In the first, the plexus consisted of seven trunks, one from each of the last two dorsals, the three lumbars and two anterior sacrals; in the second it has an additional element from the antepenultimate dorsal, but in each case the first nerve to enter the complex was that of the 14th dorsal, indicating in the case of the specimen with but 15 dorsals that the 16th had been lost. Thus there is the same number of nerves in the plexus in both animals, notwithstanding that the Proechidna has an additional lumbar. The difference lies in the fact that only one dorsal enters the complex in the Proechidna. The fact that there are but two sacral nerves to enter the plexus in both the Echidna and the Proechidna lends weight to the contention of Gregory (1910, p. 152) that the number of true sacrals in both genera is two, and that the third or last sacral is really a modified caudal. On the other hand the three vertebrae usually considered sacrals have their transverse processes entirely united with the dorsal edge of the ilium and in this respect appear together to constitute the sacrum.

## OSTEOLOGY.

In their original description of the *Proechidna* Peters and Doria (1876) figured the imperfect cranium on which they based the species. The adult skeleton was next described and well figured by Gervais (1877-'78) in the first part of his *Ostéographie des monotrèmes*. Dubois (1881) has figured the skull and the bones of the limbs, and in a later paper (1884) the elements of the sternum. He also gave brief notes on the skeleton. Thomas (1885, 1887, 1907, 1907a) has given cranial measurements of specimens in the British museum, and Weber (1888) has figured and described other adult skulls. The present discussion is confined to a summary of these notes together with such additional observations as I have been able to make on three other adult skeletons and the skulls of five younger specimens.

**SKULL.**—The cranial sutures close early, and by the time that full size is attained, they have become nearly obliterated, although the other bones of the body are still incompletely ossified. Adult crania are therefore practically solid like those of birds, except that the ring-like tympanic bones remain separate from the rest of the skull. The seven crania in the collection of the Museum of Comparative Zoölogy represent several stages in this progressive ossification from that in which nearly all the sutures are evident, to that in which all have disappeared. The homology of the several bones, owing to the difficulty of obtaining specimens young enough to show the sutures, is still somewhat unsettled. Sixta (1900) endeavored to homologize the cranial elements of the adult Echidna with those of certain reptiles but van Bemmelen (1900) showed that this was only possible after a study of young skulls. The latter author and Lubosch (1906) have written on the monotreme skull and appear to have elucidated the main points. Our *Proechidna* material, however, seems to throw additional light on a few doubtful questions, and presents other details of value.

The occipital and parietal regions of the brain-case are most developed, a condition which Gregory (1910) notes as primitive among mammals. The exoccipitals are large; the dorsal and lateral margins of each are nearly at right angles where they meet dorsal to the condyles. The large supraoccipital slightly exceeds in breadth the combined width of the exoccipitals, with which it forms the posterior face of the skull. There is considerable variation in the degree to which these three bones share in forming the superior margin of the

foramen magnum. In one specimen (M. C. Z. 12,415) the exoccipitals meet in the median line and wholly exclude the supraoccipital from the foramen. In a second immature skull (M. C. Z. 7,398) this bone is likewise wholly dorsal to the exoccipitals, but the latter do not quite meet in the median line so that a deep and narrow emargination is left between them, extending dorsally from the foramen magnum to the median edge of the supraoccipital. In an adult skull belonging to the United States national museum, a similar condition seems to exist, for there is a narrow rounded emargination of the foramen at its median dorsal border. Although all sutures are obliterated, there can be no doubt that this emargination is due to the failure of the exoccipitals to meet ventral to the supraoccipital. In a fourth specimen (M. C. Z. 7,010) the last-named bone does reach the foramen magnum and forms its dorsal border between the exoccipitals, for a space of about 3.7 mm. Like variations are recorded by Weber (1904) in this animal and similar conditions occur in the skull of the Echidna. At one time these differences were even regarded as of taxonomic value.

Abutting against the entire anterodorsal edge of the supraoccipital and extending forward nearly to the nasal region is a large median bone which is generally considered the homologue of the interparietal. It covers the greater portion of the dorsal part of the head and extends laterally nearly or quite to the dorsal margin of the large bone forming the posterior part of the zygomatic arch. It seems to be an unpaired bone, although cranium M. C. Z. 7,010 shows a trace of a small suture-like mark posteromedially.

The frontals are rather small anteriorly and expand laterally to form the dorsal two thirds or more of the orbit. Between them, posteromedially, there appears in at least two specimens (M. C. Z., 7,009, 7,010) a small separate bone, of nearly oval outline. A similar bone seems to have been discovered by van Bemmelen in the Echidna "als selbstständiger Knochenkern in vorderen Theil der sogenannten Parietalplatte des Primordialcranium." I have found what seems to be a homologous bone in a number of specimens of immature gophers (*Geomys*). Its presence is due perhaps to some irregularities of ossification. In the Proechidna it fills a small space left where the frontals and the anterior emargination of the interparietal fail to come together. For lack of a better name I have called it an interfrontal. This bone is quite different from the so-called postfrontals of Sixta and Lubosch. The latter lie one at each side of the large interparietal directly posterior to the frontals, and help to form part of the lateral wall of the cranium. At their posterodorsal angle they meet

the lateral angle of the supraoccipital. There can be little doubt that these represent the parietals of other mammals, which through the extraordinary development of the median interparietal, have here become forced apart and occupy an inferior and lateral position.

In the Echidna and especially in the Proechidna the parietal is nearly covered underneath a large vertical expansion of the posterior end of the zygomatic arch. This (Plate 2, fig. 8, *j*) is a flat scale-like bone, prolonged anteriorly into a pointed process that articulates with the dorsal surface of a long narrow extension of the maxilla to form the zygomatic arch. Its posterior expansion is nearly semicircular in outline and dorsally may be in contact with the lateral edge of the interparietal. Ventrally it is extended slightly, at right angles to its lateral face, and lines the glenoid fossa for the articulation of the jaw. At its posterolateral edge it has an emargination where the external carotid enters, and passes forward to the orbit through a canal which thus runs between this scale-like expansion and the underlying bony wall of the cranium. This is the "temporal canal," considered a unique feature in mammals and doubtfully homologous "with a similarly placed canal in Anomodonts" (Gregory, 1910). This flat scale-like bone, perhaps as much from its shape as its position, is generally considered a squamosal. In immature skulls it is easily removed exposing the underlying parietal and a second bone that occupies the wall of the cranium between the parietal and the lateral margin of the exoccipital, a bone considered by van Bemmelen the "mastoid." If this flat scale-like bone be interpreted as a squamosal, it becomes necessary to conclude (1) that the jugal is quite wanting and (2) that the so-called "squamosal" does not form part of the brain-case, as can be shown in young specimens only. The first character is highly aberrant and the second apparently unique among mammals. Van Bemmelen endeavors to overcome the second difficulty by considering the bone underlying the supposed squamosal, as a greatly developed mastoid portion of the periotic. It seems, however, that another and simpler interpretation is possible. Had van Bemmelen been able to flake off this "squamosal," he would have found that the "mastoid" extended forward from the exoccipital to the posterior margin of the parietal. At its ventrolateral border it becomes hollowed underneath the articulating surface of the glenoid cavity formed by the extension of the "squamosal." The so-called "mastoid" bone, in short, seems to fulfil all the requirements of a true squamosal and fuses ventrally with a mastoid portion that lies on the ventral wall of the brain-case lateral to the basioccipital.

If this interpretation be allowed, it is evident that the so-called "squamosal" is a greatly expanded jugal that has become flattened and appressed against the wall of the brain-case so as to obliterate almost completely the temporal fossa, of which the temporal canal for the passage of the external carotid is the only vestige. In *Ornithorhynchus* the posterior portion only of the jugal is applied to the brain-case so that the canal is very short and the orbitotemporal fossa nearly open. Further evidence is afforded by the muscles, for the temporalis, which inserts usually on the jugal, is inserted on the zygomatic portion of this bone, and the digastric, which usually originates anteriorly from the mastoid region, is in living monotremes found arising from what is here considered the true mastoid or squamosomastoid, not from what van Bemmelen considers the squamosal. Against this hypothesis is the belief of van Bemmelen that the process on the anterior dorsal edge of the arch in *Ornithorhynchus* is a true processus frontalis, and he further adds that in a young skull he found this process separated by a slight suture from the processus jugalis squamosi. In a second young skull, however, he found no such condition. It seems eminently probable that this process in *Ornithorhynchus* is not the homologue of the frontal process in higher mammals, but a dorsal extension of the maxillary portion of the zygoma. Perhaps a more serious objection to the above interpretation is that the glenoid cavity is entirely lined by an inward extension of the jugal. That the jugal should share in the formation of the articulating surface, however, need prove no difficulty, for such a condition obtains, though in much less degree, among the Marsupialia. Thus in the Giant kangaroo (*Macropus giganteus*) the posterior extension of the well-developed jugal lies against the ventral border of the squamosal process and actually forms part of the articulating surface for the broad condyle of the jaw. In other marsupials (*e. g.* *Didelphys*) this extension merely reaches the glenoid cavity and forms its lateral boundary. It is not difficult to conceive of its extension to cover the floor of this cavity as it appears to do in *Proechidna*. Moreover, Gaupp (1908) has figured this bone in a partial reconstruction of the primordial cranium in the embryo *Echidna*, and at this stage apparently, there is no inward extension to the glenoid cavity; the bone seems too far anterior to the mastoid region to fulfil the requirements of a squamosal. It is further of interest to note the tendency to a posterior dorsal expansion of the jugal in certain other marsupials so that with the ventral extension a V is formed into which the squamosal process fits. This dorsal arm is probably the homologue of the broad scale-like expansion which in the *Proechidna* covers the lateral wall of the brain-case,

and in *Ornithorhynehus* forms the narrow bridge across the temporal canal. What seems to be an analogous condition is found in certain other groups, as in the Cervidae, the Bovidae, and such Carnivora as *Mungos* (= *Herpestes*) in which the frontal process is largely developed at the posterior end and by fusion with the postorbital process makes a complete bony orbit and separates the temporal fossa posteriorly. The temporal canal in existing monotremes is thus the temporal fossa greatly restricted by the scale-like expansion of the posterior part of the jugal. In the *Echidna* this expansion is divided dorsally by a rather deep notch into an anterior and a posterior lobe, the former of which overlies the ventral edge of the parietal. In the *Proechidna*, the notch is much less evident, the dorsal outline of the jugal more nearly hemispherical and the anterior end extends far enough forward to overlap the posterior corner of the frontal.

Except for differences in relative size and form the bones of the palatal and rostral regions are essentially similar in the *Echidna* and the *Proechidna*. The termination of the palatals is slightly different, however, in the two. In the former the medial portion of the palatal is produced posteriorly as a prominent spine beyond the union with the pterygoid and there is a deep narrow reentrant between the two palatals. In the *Proechidna* one specimen shows a practically similar condition but in five other specimens the reentrant is broad and shallow, and the palatals are rounded or truncated so as to merge with the posterior outline of the pterygoids.

The nasals in the *Echidna* do not extend posterior to the margin of the orbit, whereas in the *Proechidna* they extend back to a point nearly opposite the middle of the orbit. Since they overlap the frontals for nearly a centimeter at this point, the latter bones appear for an absolutely shorter distance on the dorsal aspect of the skull than in the *Echidna*. In both, the nasals taper distally to a median point at some distance behind the nasal aperture, so that this latter is bounded entirely by the premaxillaries which meet and unite dorsally. The exclusion of the nasals from forming part of the boundary of the nasal aperture is a singular and unique condition to which apparently no attention has hitherto been paid. It is probably a specialized development, in part an accompaniment of the elongation of the rostrum. In the *Echidna* the distance from the nasal aperture to the tip of the nasal bones is one fourth of the length of the nasals. In the *Proechidna* it is slightly more than half their length, thus indicating the relatively greater development of the rostrum in the latter animal. In other mammals in which the rostrum is greatly prolonged, for example the

Great anteater (*Myrmecophaga*), the nasals have kept pace with the growth of the snout and appear at the dorsal side of the nasal aperture. Apparently in *Ornithorhynchus* these bones are not thus excluded by the premaxillaries which in this animal form the sides and anterior boundary of the opening.

The series of skulls of the *Proechidna* shows certain features of interest in regard to the order in which the sutures close. In the youngest specimen (M. C. Z. 7,009) all the chief sutures are discernible with little difficulty, and the broad jugal bones are so slightly fused with the cranium that they came entirely away in cleaning. The sutures of the occipital portion of the skull are especially clear, and the small median interfrontal is distinctly outlined. In a second specimen (M. C. Z. 7,010) of practically the same size, the premaxillaries are thoroughly fused in the dorsal midline, from the tips of the nasals to the nasal aperture, and the nasals are fused along their median line of contact though still separate laterally from the surrounding bones. The interfrontal is also with great difficulty to be traced, and the anterior edge of the large interparietal is beginning to coalesce medially with the frontal. At the occipital region of the skull the condylar portion of the basioccipital has become fused with that of the exoccipital though elsewhere the occipital sutures are broadly open. The parietal sutures are disappearing and the jugal is merging into the cranial wall. The other sutures are still traceable. A third skull (M. C. Z. 12,415) has attained adult size and shows an advance in ossification. In dorsal aspect the only sutures visible are:— the lateral and dorsal sutures marking off the exoccipitals, the lateral suture bounding the supraoccipital, the suture between the jugal and the maxillary process of the zygoma, and the sutures delimiting the maxillaries from the frontals, nasals, and premaxillaries. The nasals are solidly fused together and to the premaxillaries, though these are still distinct laterally and ventrally from the maxillaries. Conspicuous roughened furrows are developed on the vertex of the cranium for the attachment of muscles, and the posterior expansions of the jugals are solidly fused with the skull. In ventral aspect, the posterolateral boundaries of the basioccipital are quite obliterated but elsewhere the sutures delimiting this bone are still open, so that in appearance the basi- and exoccipitals are fused into a single bone whose boundaries are everywhere distinct. The bones of the palatal area are still unfused, but those of the orbit have become well soldered together.

As in the *Echidna* the palatal branch of each premaxilla becomes much drawn out posteriorly and extends as a narrowly tapering process to the origin of the zygomatic portion of the maxilla. This bone seems to increase slightly

in length up to the time when the premaxillaries fuse dorsally, after which there is practically no change in its length. The continued elongation of the rostrum seems thereafter to take place by growth at its basal portion so that the termination of the premaxillary is carried progressively farther forward from the ventral margin of the orbit. This is in accord with the fact that the sutures at the base of the rostrum are the last to close in the dorsal view of the skull. Thus in a partly grown skull M. C. Z. 7,010, in which the premaxillaries have fused dorsally, their extreme ventral length is 73 mm., and from the posterior tip to the orbit is 12.5 mm. In the fully grown skull, M. C. Z. 12,415, in which these sutures are still visible, the extreme length of the premaxillary branch is 74 mm., practically as in M. C. Z. 7,010, but from its posterior tip to the orbit is 29 mm., indicating that later growth has been entirely at this basal portion of the rostrum. The premaxilla at the same time has been carried forward and a line is left in posterior continuation of the cleft into which its tip fits.

*Cranial Measurements of the Proechidna.*

	Type	12,415	12,414	22,992	7,010	7,398
Greatest length	—	172	178	182	143	146
Basal length	—	161	167	169	134	136
Palatal length (from posterior process)	—	145	152	156	120	122
Tip of rostrum to orbit ventrally	108	103	109	113	85	84
Least interorbital width	19	19	20	19	20	20
Greatest width of brain-case	56	55	55	55	54	52
Anterior margin of orbit to temporal canal	—	45.5	44.5	41	43	41.5
Greatest length of mandible	—	130	138	139	111	110

Two quite adult skulls have also been studied. These are of the size of M. C. Z. 12,415 but show a stage farther in ossification. The first (12,414) is in the collection of the Museum of Comparative Zoölogy; the second (22,992) is in the collection of the United States national museum. In both, the sutures are totally obliterated, and the crania are solid masses of bone, except that the tympanic rings (wanting in 22,992) have not fused with the rest of the skull. Rugosities are developed for muscle attachment on the vertex of the skull, and just back of the orbit a slight ridge or process is developed on the frontal which may be considered a postorbital process homologous with that of other mammals. A small swelling opposite it near the anterior end of the jugal defines the orbit, back of which the broad plate-like expansion of the jugal covers over nearly all of the temporal fossa. The rami of the lower jaw though

closely applied along the symphysis for some 40 mm., are not ankylosed, but doubtless remain separate throughout life. The measurements of three adult skulls and two smaller and more youthful examples, as well as those of the type as given by Peters and Doria (1876) are tabulated on page 296. Thomas (1888) gives dimensions of two skulls in the British museum.

Gervais (1877-'78) in his account of the osteology of this animal figures two skulls. The first is shown in his Plate 9, fig. 1, of natural size, and is of almost exactly the same dimensions as M. C. Z. 12,415 given above. No sutures are indicated and it is doubtless the skull of a nearly mature animal. Gervais considered it the skull of a male. In his Plate 7, figs. 1-1b, are shown three views of a larger skull, of natural size, which if correctly drawn, indicate a larger animal than either of the old examples here noticed. The greatest length of the skull, as measured from these figures is 197 mm.; basal length, 187; palatal length, 174±; tip of rostrum to orbit, 129; least interorbital width, 19; greatest width of brain-case, 57; anterior margin of orbit to temporal canal, 43; greatest length of mandible, 153.

The hyoid apparatus of the Proechidna appears to be still undescribed. The larynx is situated far posteriorly on the throat and the hyoid bones are few and small (Plate 2, fig. 7). The basihyal is relatively broad and bears at each end on its anterior face a cephalic cornu of two pieces, the basal of which probably represents a ceratohyal. The more distal piece is of about half the size of the latter and tapers to a point which is connected by tissue with the sides of the pharynx. No tympanohyal articulating the larynx with the skull appears to exist. At the posterior face of each end of the basihyal, a large thyrohyal passes dorsally to the cephalic cornu of the thyroid cartilage. The cricoid cartilage joins the thyroid by a common median cartilage, though a faint transverse line probably indicates the original separation of the portion proper to each ring. The more ventral portions of thyroid and cricoid are bony. The arytenoid processes are produced backward as a long tapering cartilage to the dorsal end of the cricoid. Following the cricoid is a large, nearly complete tracheal ring, succeeded by the trachea, which consists of some 18 or 19 cartilaginous pieces not quite complete dorsally.

VERTEBRAE.—The vertebrae of the Proechidna have been well figured by Gervais (1877-'78) and their general character is as in the Echidna. The first seven (cervicals) have a complete vertebral arch, formed by the union of the cervical rib with the transverse process and the centrum. In old individuals these ribs become solidly fused with their respective vertebrae. Such true

cervical ribs are regarded as primitive. The succeeding ribs are attached by their capitula only, since the tubercula are wanting and articulate by demi-facets with two contiguous vertebrae. An anomalous feature in monotremes is the perforation of the neural arches of the dorsal and succeeding vertebrae by their spinal nerves, which usually issue from between the vertebrae in other mammals. According to Gregory (1910) this seems to be a unique feature.

The vertebral formula for the Proechidna is given by Gervais (1877-'78) as:— C 7, D 17, L 4, S 3, Ca 12 = 43 which is thus one dorsal and one lumbar more than ordinarily assigned to the Echidna. This is the vertebral formula commonly ascribed to the Proechidna, and the additional vertebrae are considered as forming an important generic character. No new observations as to the vertebral formula have been published except that Dubois (1884) in urging that 17 instead of 16 pairs of ribs may be considered one of the generic characters, adds that a skeleton examined and briefly described by him had but 16 pairs. Two of the specimens in the collection of the Museum of Comparative Zoology are accompanied by nearly complete skeletons, both of which were carefully cleaned by the writer; in addition the mounted skeleton belonging to the United States national museum has been studied. From these various sources, the following data are derived as to the vertebral formula:—

Gervais (1877-'78): C 7, D 17, L 4, S 3, Ca 12 = 43.

Dubois (1884): C —, D 16, L —, S —, Ca — = —.

M. C. Z. 12,414: C 7, D 16, L 4, S 3, Ca 12 = 42.

M. C. Z. 12,415: C 7, D 16, L 4, S 3, Ca 11 = 41.

U. S. N. M. 22,992: C 7, D 16, L 5, S 3, Ca 12 = 43.

As was perhaps to have been expected there is a slight amount of variation. The usual seven cervicals are present in all the cases known; but in the Echidna there is variation even here, for Broom (1900) has recorded a case in which eight cervicals were present. Four of the five specimens have 16 dorsals and the fifth has 17, so that the usual number may fairly be considered 16 as in the Echidna. An additional young specimen in the collection of the Museum of Comparative Zoölogy, has, however, but 15 pairs of ribs. The interpretation of the lumbar and sacral vertebrae appears to have offered some difficulty. In the Echidna these are generally considered to be three each. Gregory (1910, p. 152) writes:— “Howes (1885, p. 89) gives 4 sacrals to *Echidna* and 3 to *Ornithorhynchus*. In that case both genera would have 19 dorsolumbar vertebrae (*Proechidna* 20) a number characteristic of primitive Marsupials.” In Gregory's opinion, however, “the anterior ‘sacral’ is only a slightly modified lumbar and

the posterior sacral only a slightly modified caudal." He assigns to the Echidna the formula, C 7, D 16, L 5, S 2, —, Ca 10 = 40. In the skeletons of the Proechidna studied, there seems no reason to doubt that three is the number of functional sacral vertebrae in each, anterior to which in M. C. Z. 12,414 and 12,415 there are four undoubted lumbars. In M. C. Z. 12,414, an old individual, four vertebrae enter into the fused sacral mass, but the most posterior of these is very evidently a caudal that has become thoroughly united by its centrum and articular processes to the last sacral, and by its transverse processes to the posterodorsal margin of the ilium. It is therefore reckoned as a caudal. Evidence for the belief that the saerum includes morphologically but two vertebrae is found in the fact that but two and these the anterior two sacral nerves enter into the lumbosacral plexus. Gervais considered four and three the numbers respectively of lumbars and sacrals in his specimen, so that these may be considered the normal number of each. In the skeleton belonging to the United States national museum, however, there are five lumbars in addition to the three sacrals, evidently an unusual condition. The caudals, as in the Echidna seem usually to be 12 in number, though one (M. C. Z. 12,415) had but 11. There are six chevron bones, the first of which comes between the third and fourth caudals. They are simply small oval ossicles, of which the second is the largest and from it the remaining four form a diminishing series. The usual vertebral formula for the Proechidna may therefore be considered as C 7, D 16, L 4, S 3, Ca 12 = 42, which differs from that of the Echidna in having four instead of usually three lumbars, although even this difference may disappear, since four lumbars are said to occur in the Echidna in certain instances. Thus McKay (1894) has tabulated the vertebrae of eighteen specimens of the Australian Echidna and shows that the range of variation is considerable, namely, cervicals 7, dorsals 14 to 17, lumbars 2 to 4, saerals 3 to 4, caudals 10 to 12. It thus appears that no generic difference in vertebral formulae exists, as once supposed, between the Echidna and the Proechidna for the range of individual variation bridges over the gaps.

**RIBS.**—Six of the ribs articulate directly with the sternum as in the Echidna. The sternum in a nearly grown individual, consists of four rib-bearing portions. The first is the manubrium, broadly expanded at its anterior end, where the first pair of ribs meets it, and contracted posteriorly, where it is joined by the second pair. Dubois (1884) figures this first segment as ossifying in a youngish specimen of what he calls *P. villosissima* from two lateral centers. The three succeeding sternebra are slightly narrower than the posterior end of the manubrium.

The first and second support each a single pair of ribs, while the third supports the fifth and sixth pairs. This last piece thus evidently represents two sternebra fused, as indicated in addition, by a slight furrow on the sternebrum between the last two sternal ribs, marking the point of fusion. There are four remaining sternebra making nine in all, but these last are small and do not support ribs. In an old individual the five rib-bearing sternebra are reduced to three, owing to the complete fusion of the last three. Gervais's figures indicate similar conditions. The dorsal end of the sixth sternal rib is greatly expanded, and so likewise are the ventral segments of ribs 7 to 12, which overlap each the one next anterior. Ribs 13 and 14 have a cartilaginous connection only, with these bony plate-like portions, while ribs 15 and 16 are short, and backwardly directed, without particular connection with the thoracic basket.

**GIRDLES AND LIMBS.**—The characters of the pelvic and pubic girdles are in general similar to those of the Echidna as ably discussed by Gregory (1910, p. 152-153). The various elements of each are in adults thoroughly fused, although the line of union of the scapula with the interclavicle usually remains distinct. In M. C. Z. 12,414, an old animal, the line of suture is still clear between the left coracoid and procoracoid.

There can be no doubt that the Proechidna with normally three claws on each foot is a derivative from some form which like the Echidna was five-clawed. In this and certain other respects, it therefore represents a stage in advance of the condition shown by the Echidna so that as Toldt (1905) justly says, the term Proechidna is somewhat of a misnomer. Several cases are on record in which more than three claws have been noted on the foot of the Proechidna, and these must undoubtedly be considered as instances of regressive variation. On both fore and hind feet it is digits 2, 3, and 4 that are normally provided with claws. Digits 1 and 5 are usually covered by a callosity and at most are mere prominences in external aspect. Of the eight specimens in the collection of the Museum of Comparative Zoölogy, two only show more than the normal three claws on each foot. The first is a mounted specimen, 6,722, from northern New Guinea, in which there is a claw on digit 5 measuring about 19 mm. in both right and left fore feet. I suspect that there were also claws on digit 5 of each hind foot, but these if present must have become lost. The chief reason for this belief is that they exist on the fifth digits of the fore and hind feet in the United States national museum's specimen 22,992 which is the skeleton of apparently the same individual whose mounted skin is in the Museum of Comparative Zoölogy. Both were purchased independently from Ward's Natural science estab-

lishment a number of years ago. The second anomalous specimen is M. C. Z. 7,009, collected by Dr. Thomas Barbour in Sorong, New Guinea. This specimen has the usual three claws on each of the fore feet, but a small extra claw on digit 5 of each of its hind feet. This extra claw measures 9 mm. in length. There are several other cases of variation on record, as follows:—

Thomas (1907a, p. 499, footnote) records that the type specimen of his *Acanthoglossus bruijnii bartoni* had five claws on both of the fore and hind feet, as in the Echidna. Weber (1888) describes at length a specimen in Amsterdam, that had five functional claws on both fore feet, and four on each hind foot. From his figure it is seen that the supernumerary claw on the hind foot is that of digit 5, though in the text, through error, it is given as of digit 1. Its length is 15 mm., or less than half that of the fourth claw. Toldt (1906) mentions two other abnormal specimens. The first of these is in the Museum at Brussels. On digit 1 of the right fore foot is a second phalanx bearing a claw 12 mm. long. The left fore foot, however, has but the usual three claws on digits 2, 3, 4, as have also the hind feet. The second individual is in the Umlauff museum at Hamburg. The left fore foot only of this individual is abnormal in that each of the five digits bears a claw. That of digit 1 is short and rounded but that of digit 5 is more fully developed, 11 mm. long and 6 mm. broad. The six known abnormally clawed individuals of this genus may be tabulated as follows, the numeral expressing the presence of a claw on its respective digit.

*Abnormally clawed Proechidnas.*

Specimen.	Right Fore.	Left Fore.	Right Hind.	Left Hind.
British Museum	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5
Amsterdam	1, 2, 3, 4, 5	1, 2, 3, 4, 5	0, 2, 3, 4, 5	0, 2, 3, 4, 5
U. S. N. M. 22,992	0, 2, 3, 4, 5	0, 2, 3, 4, 5	0, 2, 3, 4, 5	0, 2, 3, 4, 5
M. C. Z. 7,009	0, 2, 3, 4, 0	0, 2, 3, 4, 0	0, 2, 3, 4, 5	0, 2, 3, 4, 5
Brussels	1, 2, 3, 4, 0	0, 2, 3, 4, 0	0, 2, 3, 4, 0	0, 2, 3, 4, 0
Hamburg	0, 2, 3, 4, 0	1, 2, 3, 4, 5	0, 2, 3, 4, 0	0, 2, 3, 4, 0

Since some twenty-five or more specimens are recorded in which the claw formula for each foot is 0, 2, 3, 4, 0, this must be considered the normal condition, from which regressive variation sometimes takes place. In case of the hind feet, digit 1, as might be expected from its less marked skeletal development, is much more rarely clawed than is digit 5—in fact there is but one recorded case of a claw on the first hind digit. No instance is known of its presence without also an accompanying claw on digit 5. No doubt the order of disappearance in phylogeny is first claw 1, then 5. The reduction of the fore

claws may have begun later phylogenetically, for except the British museum specimen having five claws on each foot, there is but a single case (M. C. Z. 7,009) in which the fore claws are less in number than the hind.

In normally clawed specimens, there are three phalanges in each of digits 2, 3, 4, but only two in digit 5, and one in digit 1. In the mounted skeleton belonging to the United States national museum, in which there is a claw on each digit 5, the latter has three phalanges, in each case. This extra phalanx is the terminal or claw-bearing one, and is doubtless the one that is lost in the normally clawed individuals. This is further indicated by Dubois (1881) who found in one example, three phalanges on each hind digit 5, and two on each hind digit 1. In every case the terminal extra phalanx was small, bore no claw, and evidently was a mere remnant of a once functional member.

Gervais figures a palmar sesamoid, such as is so well developed in certain edentates, but I found none in the specimen I dissected, which was probably too young.

The remaining bones of the feet and limbs are not essentially different from those of the Echidna, except that the humerus differs conspicuously in its distal outline. The internal tuberosity is broad and evenly rounded and has a comparatively shallow notch at the internal border of the articulating area. In the Echidna on the other hand, the inner tuberosity is narrower and with a deep notch in its distal margin below the entepieondylar foramen. The notch at the ental side of the articulating surface is also much deeper. It is in exactly these points that the fossil humerus of Owen's *Echidna ramsayi* (Owen, 1884, pl. 14) from New South Wales, Australia, agrees with the humerus of the Proechidna and differs from that of the Echidna. For this reason, as well as on account of its large size, I consider this extinct animal the representative of the genus Zaglossus in Australia. Although it has become extinct on that continent, it seems apparent that the genus in its restricted sense, formerly was represented there, and that through a land-bridge that has since disappeared, it reached New Guinea at the same time with the true Echidnas (*Tachyglossus lawesi*) and has there survived. With regard to the remains of this Australian Proechidna but little has been published. Krefft (1868) in a brief note, first announced the discovery of this extinct animal and figured the distal condyle of the humerus. He says that he does not wish to name it lest it may have been already described, but otherwise would call it *Echidna owenii*. Apparently this name must hold good for the species. Owen (1884) described and figured a nearly entire humerus, and later (1887) recorded that in the "Wellington bone

and breccia caves" of New South Wales, further portions had been discovered, including an entire humerus, a large portion of the skull, atlas, a tibia, and fragmentary evidences of other parts of the same skeleton." The edentulous condition, proportions, and conformation of the jaws, together with other "characteristic modifications of this monotrematous genus [Echidna], are repeated on the same magnified scale as in the mutilated arm-bone previously described and figured." The nature of these remains is not further indicated, but it seems probable that they are referable to the Proechidna, as, indeed, Flower and Lydekker (1891, p. 127) point out; they state that "In referring this species to the genus *Echidna*, that term must be regarded as including *Proechidna*." The fossil humerus as figured by Owen (1884) is but very little longer than that of an adult New Guinea Proechidna.

SPUR.—Gervais found a spur on but one of his two specimens, the one by him regarded as a male. It is generally considered absent in the adult female as is true also of the Echidna and the Duckbill. Thus Toldt (1905) found no spur in one of the Vienna proechidnas he examined, while a second had a rudimentary one only. In two alcoholic specimens in the Museum of Comparative Zoölogy, that were males by dissection, the spur was well developed. It is slightly attached by connective tissue at the tarsus, but I was unable to discover any trace of a gland or duct in connection with it, such as is described for the Duckbill.

## HABITS.

Practically nothing is known of the habits of the Proechidna in a wild state. According to A. A. Bruijn, by whom the original cranium was sent to Peters and Doria, the specimen was found by a native hunter on Mt. Arfak, at a considerable altitude. Here the animal was said to be not rare, living in burrows; the natives hunted them by the aid of dogs, and were fond of their flesh. The hairy coat was said to be long and very harsh. Gervais had two specimens from the Karon Mountains, northern New Guinea, at an altitude of 1,150 meters. The natives called it *nokdiak*. In British New Guinea, a specimen is recorded by Thomas (1907) from Mt. Victoria at an altitude of 8,000 feet, and is made the type of the race *bartoni*. Guillemard (1886) writes that his native hunters at Doreh Bay obtained a specimen for him, and that it was said to live in burrows in rocky ground. It is doubtless an inhabitant of rocky places, and therefore avoids the low country along the coast, but present evidence does not indicate that it is confined to high altitudes. Dr. Thomas Barbour in 1906

obtained two living Proechidnas from the natives at Sorong, a small low lying island which is separated by a shallow and narrow strait from the Papuan mainland. These were both captured by a party of Papuans who had been on an excursion to the hills which lie a few miles back from the swampy coastal plain bordering the mainland shore.

One of Dr. Barbour's specimens (both of which he has presented to the Museum of Comparative Zoölogy) was in good condition and he has kindly written the following account of it:—"This specimen was kept alive for about a month and a few observations on its habits were made. It was absolutely nocturnal and spent the day partially buried in the deep layer of sand which was kept in its cage. It slept rolled up with its snout turned directly under its chest and covered by the fore limbs. When aroused and taken out in daytime, it would lie flat on its stomach with its snout stretched out resting on the ground. If disturbed, it at once turned its snout under it and raised a heavy fold of skin that moved down over the forehead and protected it by carrying forward a heavy armament of spines. The subdermal musculature is remarkably strong and effective, causing the spines to be quickly turned and rigidly held in any direction. At night it moved about sluggishly, often digging with motions that strongly recalled those of a turtle. It fed on ants only, which were procured by placing in a dish a considerable amount of shredded cocoanut. The ants soon swarmed in this and the whole was then placed in the Proechidna's cage. It ate the insects by thrusting its long tongue down into the cocoanut. It took a little water or water with condensed milk, but seemed to drink very little."

Most of the specimens of Proechidna come from Dutch New Guinea—Mt. Arfak (type locality), Karon Mountains, Doreh Bay, Sorong, the hilly country between Fak Fak and McCluer Gulf; specimens are also recorded from the Finisterre Mountains of German New Guinea and from Mt. Victoria, British New Guinea. A specimen (*goodfellowi* Thomas) from the island of Salawatti, really a part of western Dutch New Guinea, is doubtless identical with the Proechidna of the mainland.

#### SUMMARY AND CONCLUSIONS.

The foregoing account is based on a larger series of skins accompanied by skulls than has ever before been brought together, while in addition four skeletons have been examined and dissection made of an alcoholic specimen.

From a comparison of these as well as from a careful study of the

descriptions of the five described forms or species of the Proechidna, the conclusion is reached that all are referable to a single living species, namely *Zaglossus bruijnii*, of New Guinea, and that the various nominal races are based on individual variations due to age, wear, albinism, or individual differences in pigmentation and molt.

On account of the size and conformation of the humerus figured for the extinct *Echidna owenii* of New South Wales, it seems that this animal should be referred to the genus *Zaglossus*, thus establishing the occurrence of both *Zaglossus* and *Tachyglossus*, the Proechidna and the Echidna, in Australia as well as in Papua.

The musculature is essentially like that of the Echidna, but that of the limbs shows important differences correlated with the reduction of the functional digits from five to three. Thus the *flexor profundus digitorum* sends tendons to digits 2, 3, and 4 only, and no trace is left of the additional tendons to 1 and 5 that are present in the Echidna with its five-clawed manus. There is also in the hand a muscle apparently representing the *abductor digitii quinti*, which seems to be absent in the Echidna. The *adductor longus* is present in the hind leg of the Proechidna but apparently is lacking in the Echidna, and a small muscle probably representing a *flexor longus hallucis* is also found, but is absent in the Echidna.

In correlation with the elongation of the beak, the tongue and salivary glands are more developed in the Proechidna. No second portion of the submaxillary gland was detected. There is a common duct by which the gall-bladder and the pancreas enter the intestine, not two separate ducts as described for the Echidna by Chapman.

The supposed differences in vertebral formulae between the Proechidna and the Echidna are shown to be unreliable. Both exhibit a considerable degree of individual variation. A study of the young skull reveals several interesting peculiarities, such as a small median bone formed posteriorly between the frontals and here called interfrontal. The nasals are shut off from the external narial opening by the meeting of the premaxillaries in front of them. The zygomatic arch is shown to be formed mainly by an enormously expanded jugal, and the squamosal, which has been supposed to form the arch is really covered by the jugal and forms part of the brain-case as usual. The temporal canal of existing monotremes is merely the remnant of the temporal fossa, largely closed over by the expansion of the jugal dorsally. A ventral expansion of the jugal lines the glenoid cavity of the jaw.

Although there are normally three functional digits on each foot, six cases are recorded in which there are more than this number. These are to be considered as regressive variations to the five-clawed condition as seen in the Echidna. Only one case is known in which there were five claws on each foot.

The validity of the genus *Zaglossus* for the *Proechidna* as distinct from *Tachyglossus* for the *Echidna* has been questioned, but as modern generic concepts go, they may well be kept apart. The chief characters of *Zaglossus* are: — (1) the great elongation and depression of the rostrum, with the accompanying greater development of the tongue and salivary glands; (2) the usual possession of but three functional claws on each foot, correlated with important differences in certain of the muscles of the fore and hind legs; (3) the outline of the distal end of the humerus is very different from that of the *Echidna*, with a broad, evenly rounded inner tuberosity and a shallower notch at the ental side of the articulating surface; (4) the spines are more solid with a relatively small lumen in contrast to the thin-walled spines with large lumen of the *Echidna*.

The *Proechidna* represents a more highly specialized type than the *Echidna*.

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PLATE 1.

*Zaglossus bruijnii.*

Fig. 1.—Side view, somewhat diagrammatic, to show relations of certain superficial muscles. *al*, anterior portion of latissimus dorsi; *bf*, biceps femoris; *dfc*, dermo-flexor cruris; *el*, extensor longus digitorum; *fr*, flexor carpi radialis; *fu*, flexor carpi ulnaris; *gm*, gluteus maximus; *gme*, gluteus medius; *ie*, ilio-costalis; *il*, iliacus; *ld*, the dermo-flexor antebrachii of Fewkes, possibly a portion of the latissimus dorsi; *m*, the dermo-dorsi cerviealis, possibly a derivative of the latissimus dorsi; *p*, flexor profundus digitorum; *pe*, peroneus tertius; *pl*, peroneus longus; *pt*, pronator teres; *py*, pyriformis; *t*, trapezius; *ta*, tibialis anterior.  $\times \frac{2}{3}$ .

Fig. 2.—Extensors of the fore foot. *ed*, extensor digitorum communis; *el*, extensor digitorum lateralis; *ep*, extensor brevis pollicis; *erb*, extensor carpi radialis brevis; *erl*, extensor carpi radialis longus; *eu*, extensor carpi ulnaris; *pa*, ulnar insertion of panniculus; *pt*, pronator teres.  $\times 0.8$ .

Fig. 3.—Flexors of the fore foot. *ab*, abductor digiti quinti; *an*, anconeus; *ap*, adductor pollicis; *fb*, flexor brevis digiti quinti; *fr*, flexor carpi radialis; *fu*, flexor carpi ulnaris; *p*, flexor profundus digitorum; *pt*, pronator teres; *u*, ulna; the small interossei are shown running from the palm to the bases of the digits.  $\times 0.8$ .

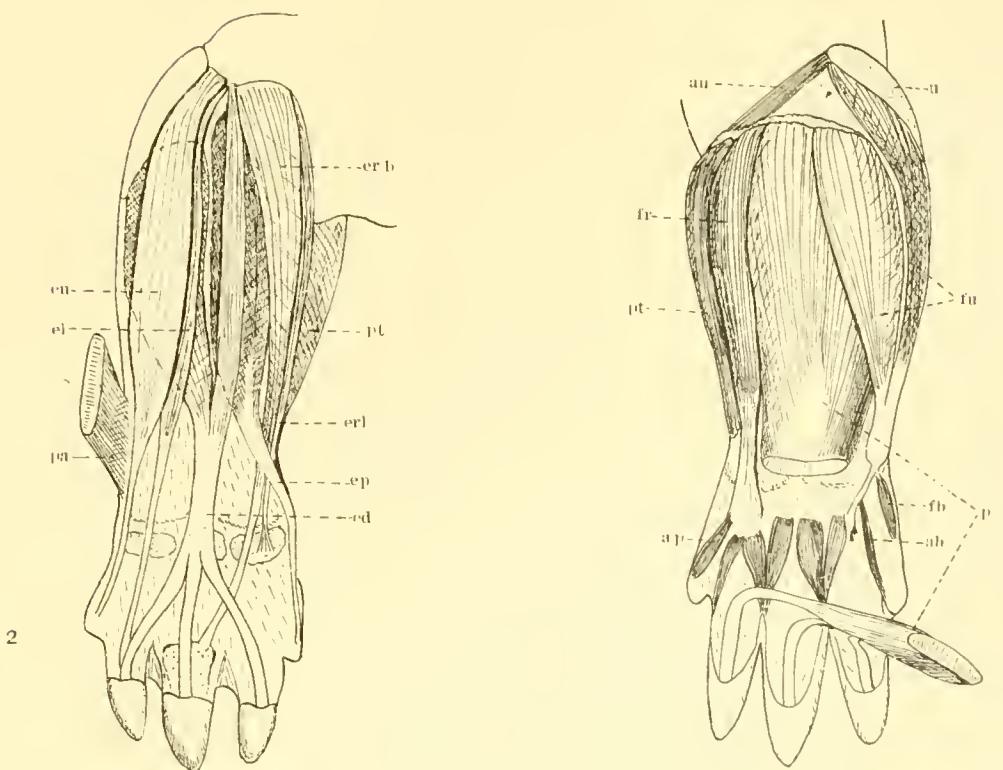
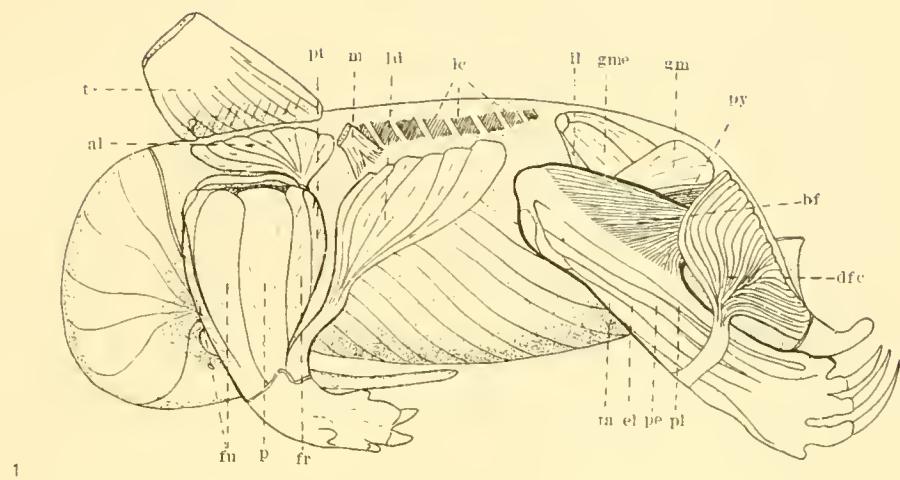






PLATE 2.

*Zaglossus bruijnii.*

Fig. 4.—Muscles of the right hind leg, ventral aspect. *af*, adductor femoris, from two heads; *al*, adductor longus; *fld*, flexor longus digitorum; *g*, gracilis (eut); *gas*, gastrocnemius; *pec*, pectineus; *pla*, plantaris; *rf*, rectus femoris; *sa*, sartorius; *sm*, semimembranosus; *so*, soleus; *st*, semitendinosus; *va*, vastus medialis.  $\times 0.6$ .

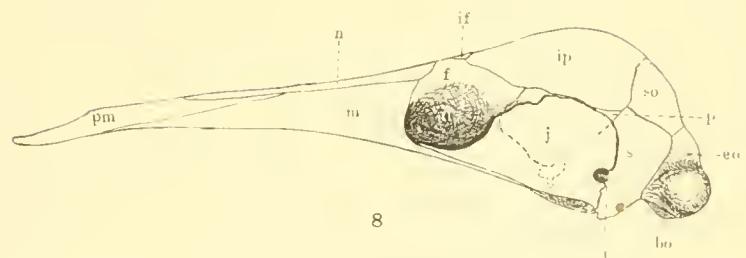
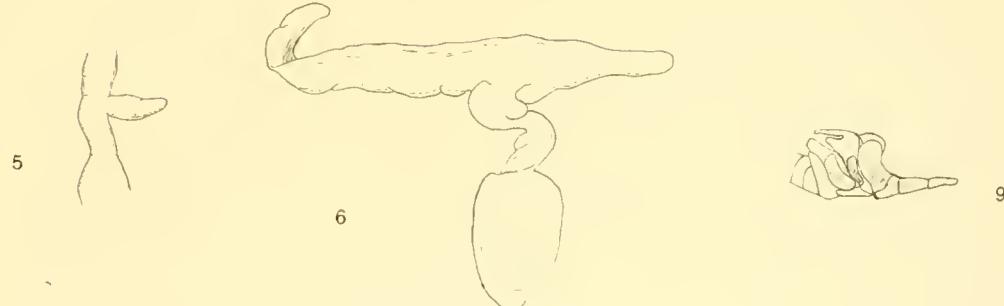
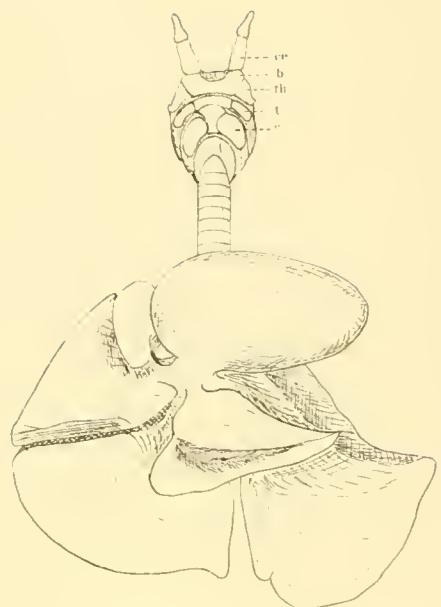
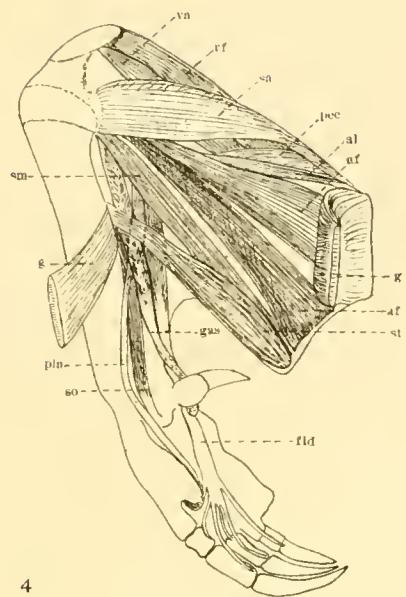
Fig. 5.—Caecum.  $\times 0.6$ .

Fig. 6.—Spleen, ventral aspect.  $\times 0.6$ .

Fig. 7.—Larynx, lungs, and heart, ventral aspect. *c*, cricoid; *ce*, ceratohyal; *b*, basihyal; *t*, thyroid; *th*, thyrohyal. The heart is turned forward, exposing the azygos lobe of the lungs.  $\times 0.6$ .

Fig. 8.—Side view of the skull of an immature Proechidna, showing somewhat diagrammatically the sutures. *bo*, basioccipital; *eo*, exoccipital; *f*, frontal; *if*, interfrontal; *ip*, interparietal; *j*, jugal, greatly expanded, covering part of parietal and squamosal; *m*, maxillary; *n*, nasal; *p*, parietal nearly covered by jugal, its outline shown by broken line; *pm*, premaxillary; *s*, squamosal, partly covered by jugal; *so*, supraoccipital; *t*, temporal canal.  $\times 0.6$ .

Fig. 9.—Larynx in side view.  $\times 0.6$ .







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